EARLY SELECTION FOR VOLUME GROWTH IN SLASH PINE

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1993

ACKNOWLEDGEMENTS

Several years ago my major professor Dr. Timothy White, and Dr. Mary Duryea made plans for initiating a large-scale early selection project. With substantial contributions from them and many other people, I have carried out the project. Tim has been a truly great major professor. He has shared his time, knowledge, and friendship with me; he takes very good care of his graduate students. Dr. Gary Hodge has been my statistics mentor over the past four years as well as serving as a committee member and I am sincerely grateful to him for his guidance and friendship as well. I also am grateful to Dr. Mary Duryea, Dr. Alan Long, and Dr. Jerry Sartain for serving on my committee. Dr. Long was also instrumental in constructing the irrigation system.

Mr. Greg Powell also deserves special recognition for helping me in the day to day operations. Of course, I cannot forget Charles Akins who has since retired, but was very instrumental in building the seedling boxes and taking care of the seedlings during the early days of this project. I want to thank current and former staff members at the Austin-Cary Forest who helped with seedling box construction and harvesting: Mike Allen, Steve Brooker, Gary Durden, Eddie Higgins, and Sam Jones. I also want to thank the three ladies who did most of the 'grunt' work in this study separating biomass components (needle and root picking), Gina Taylor, Jennifer Prentiss, and Christy Lovejoy. Finally, I thank my fellow graduate students who freely and willingly gave a helping hand: Delaney Faircloth, Dudley Huber, Kris Irwin, Carol McCormac-Wild, Deborah McGrath, Mike O'Donnell, Ken Smith, Anne Todd-Bockarie, and the department technicians: Robert Berger, Jeff English, Abbie Foxx, Harm Kok, and Winnie Lant.

I gratefully acknowledge the members of the Cooperative Forest Genetics Research Program (CFGRP) and the Georgia Forestry Commission for funding this project. I have truly enjoyed working with Tim, Mary, Gary, Greg, and the students over the past four years at UF.

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of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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August 1993

Chairperson: Dr. Timothy L. White
Major Department: Forest Resources and Conservation

This study was conducted to investigate early selection for 15-year volume growth in slash pine. Seedlings from 64 open-pollinated families of slash pine were grown under low and high nitrogen (N) treatments (5 ppm and 50 ppm) in outdoor boxes for two growing seasons. These families have been extensively tested for 15-year volume growth in the field. Approximately 360 seedling traits were measured or derived using data from several non-destructive measurements and from destructive harvests conducted at 3, 6, 10, and 18 months after sowing.

The first part of this study investigated relationships between seed weight components and seedling growth, and 15-year volume growth. Embryo weight consistently had a strong relationship with both seedling growth traits and 15-year volume growth, and may be useful as an early selection trait. Due to the strong genetic relationship between seed weight components and seedling growth, statistical adjustments for seed weight effects in slash pine might remove useful genetic variation rather than remove temporary maternal effects.

In the second part of this study, genetic parameters (i.e., family heritabilities, type A genetic correlations, and type B genetic correlations) were estimated for dry weight traits (i.e., needle, stem, taproot, lateral roots) measured at 3, 6, and 10 months. Family heritability estimates were high for all traits in all harvests ($h_f^2 > 0.70$). Type A genetic correlations, measuring the genetic similarity between pairs of traits in the same N treatment, indicated that dry weight traits have strong genetic relationships. Type B genetic correlations, measuring the genetic similarity of the same trait across the two N treatments, also indicated strong genetic relationships between traits.

In the third part of this study, selection indices were developed from over 360 seedling traits to estimate the efficiency of early selection in slash pine. Compared to direct selection for 15-year volume growth, some selection indices were more than 60% efficient. Selection indices were more efficient at predicting the bottom 25% of the population than the top 25%. An early selection technique using traits in this study would not be efficient enough to supplant progeny testing but could be used to reduce the size of field tests via early culling of poor performing families or to provide information for directed crossing among parents.

INTRODUCTION

The University of Florida's Cooperative Forest Genetics Research Program (CFGRP) is a cooperative of the university and 11 forest industry corporations and state forestry agencies working to genetically improve slash pine. Collectively, the members own or breed for over 20 million acres of commercial timberland in Florida, Georgia, Alabama, and Mississippi. Two major goals of the CFGRP are to identify and produce genetically improved varieties of slash pine for reforestation and to conduct research that increases our knowledge of the genetics of slash pine.

Towards these goals, during the early 1960s, the CFGRP selected over 2,000 slash pine trees from natural pine stands based on their **phenotypic** appearance. Due to large environmental effects (such as microsite differences in soil, competition, localized inbreeding, and other stand-to-stand variations), their phenotypic appearance poorly reflected their genetic potential (i.e., low heritability). Therefore, their progeny were grown on many different sites (field or progeny testing) with proper experimental designs to facilitate selection based on genetic quality.

In this first generation of improvement, over 300 field tests were established and measured several times until age 15 at a substantial cost. Currently, the breeding generation interval in the CFGRP is approximately 13-15 years; evaluation for parental worth is at age 8-10 and breeding procedures add another 5 years (White and Hodge 1993). Considering the resources spent in maintaining large numbers of field tests for long periods, it is very important to identify traits early in the tree's life cycle to facilitate earlier genetic evaluation or reduction of test sizes. If traits can be found in seedlings at one or two years of age that are predictive of later tree growth in operational field environments, then this could both reduce costs (by reducing size and/or number of field tests) and increase genetic gains (by allowing earlier selection and therefore more rapid turnover of generations). The CFGRP has selected 933 second-generation genotypes of slash pine which will require field testing beginning in 1995. Unless an early selection procedure can be developed for slash pine by that time, evaluation of these selections may require amounts of resources comparable to the first generation of improvement.

Most tree improvement programs for conifer species have investigated the feasibility of early genetic evaluation. A vast majority of studies have had limited success; the results have not been conclusive enough to warrant operational early selection. There are numerous reasons for the failure of early selection studies, but I will focus on the four main problems. First, a large number of families and individuals are critical for accurate prediction of juvenile-mature correlations (Lambeth 1983). Testing a few families and/or a few seedlings per family may yield imprecise estimates of juvenile-mature correlations. For reliable estimates of genetic parameters, many families (50 or more) are required (Huber et al. 1992). Second, when calculating juvenile-mature correlations, many studies (particularly earlier studies) have used imprecise estimates of the mature trait rather than precisely estimated additive genetic breeding values derived from testing across many field sites.

Third, most studies have not addressed seed effects which may have a confounding influence on the genetic analysis of early seedling growth leading to biased estimates of heritabilities and genetic correlations (Lambeth 1983, St. Clair and Adams 1991). Fourth, choice of seedling growing environment is critical to maximize the predictive ability and some believe that seedling environments should simulate natural conditions (Waxler and van Buijtenen 1981, Williams 1988).

Finally, genophenotypic or family mean correlations with the target traits have been estimated for single juvenile traits. Multiple-trait selection indices combining several juvenile traits will likely provide better predictive ability for the mature trait than single-trait correlations (Foster 1986), particularly if the juvenile traits are correlated with the target, but not phenotypically correlated with each other (White and Hodge 1991).

In this study, attempts were made to circumvent some of these problems by a) using a large number of families (64) which have already been extensively field tested for volume growth, b) using best linear prediction to make precise predictions of the parental breeding values for field volume growth (White and Hodge 1988), c) growing the seedlings in two distinct nitrogen (N) environments known to alter seedling trait expression and simulate natural conditions (DeWald et al. 1992), d) analyzing combinations of two- and three-trait selection indices to predict field breeding values and e) addressing the effects of seed weights on early selection traits and field breeding values.

The first chapter focuses on the effects of seed weight characteristics on seedling growth and long-term field growth. The goals were 1) to examine relationships among seed weight components and seed size classes, 2) to estimate the magnitude of seed size effects and germination vigor on three key seedling growth traits during the first two growing seasons, and 3) to evaluate seed weight components as potential genetic selection criteria for predicting 5- and 15-year volume growth.

The second chapter focuses on genetic parameters estimates of seedling dry weights. The goals were 1) to estimate family heritability for seedling dry weight traits in limiting (simulating natural conditions) and non-limiting N treatments, 2) to estimate genetic correlations among the traits, and 3) to evaluate all traits singly and in all possible combinations (across three different harvest dates and two N levels) to predict 15-year breeding values for volume growth.

The third chapter employs traits from the first two chapters, traits from relative growth rate and nitrogen use efficiency analyses, and traits measured by Smith et al. (1993a and 1993b) to develop operational indices for early selection. The goal was to identify combinations of easily measured seedling traits that were effective enough to either supplant field testing, to reduce field test sizes, or to direct future breeding efforts.

RELATIONSHIPS AMONG SEED WEIGHT COMPONENTS, SEEDLING GROWTH TRAITS AND PREDICTED FIELD BREEDING VALUES IN SLASH PINE

Introduction

Seed size effects on seedling growth, typically strong during the first growing season, but then declining, have been observed in many conifer species including Douglas-fir, (St. Clair and Adams 1991), Scots pine, (Wrzesniewski 1982, Mikola 1984), loblolly pine, (Shear and Perry 1985, Waxler and van Buijtenen 1981), Caribbean pine, (Toon et al. 1991), and slash pine (Langdon 1958, Shoulders 1961, Bethune and Langdon 1966). Seed size effects on seedling growth may be induced by physiological and morphological differences among seeds of different sizes. Large seeds, presumably having more storage materials in relation to embryo size, better developed embryos (Wrzesniewski 1982), higher levels of plant growth regulators (Krugman 1965), and less restriction to water imbibition than smaller seeds, may germinate more rapidly (Dunlap and Barnett 1983) and may be less susceptible to pathogens (Boyer et al. 1985).

Variation in seed size both within and among families is largely due to effects associated with the maternal tree (St. Clair and Adams 1991). In loblolly pine, for example, female parents account for about 90% of the total variation in seed size (Perry 1976). The maternal tree influences seed development by determining the genetic composition of the seed coat (diploid maternal) and the gametophyte (haploid maternal) and by its environmental effect during seed development. Because the embryo typically occupies only about 10% of the total size, the paternal parent contributes little to variation in total seed size (Perry 1976).

Seed size effects may confound results in physiological and genetic research on seedling material. Righter (1945) suggested that genetic differences among seedlings would be manifested more efficiently if embryos could be planted without seeds. In studies using classical growth analysis, differences in initial seedling size induced by seed size differences may result in smaller seedlings having higher relative growth rates than larger seedlings (van den Driessche 1992). In addition, seed size effects can contribute to the among-family variance and thus inflate the observed genetic variance in seedling growth, leading to biased estimates of heritability and genetic gain. For example, in Douglas-fir seedlings, upward bias in genetic gain for three seedling traits ranged from 10% to 45% (St. Clair and Adams 1991). With knowledge of the relationship between seed size and seedling growth, statistical adjustments can be employed to improve the correlated response from early, indirect selection.

The study of seed properties also provides an opportunity to evaluate seed traits as possible selection criteria. If genes involved in seed development are linked or pleiotropic with other traits, implying a genetic correlation, then seed traits can be used in a selection index. For use in a selection index, seed traits must be either genetically correlated with field breeding values themselves or correlated with other traits which are predictive of field breeding values (White and Hodge 1991). Long-term relationships between seed weight and growth traits have been observed in loblolly pine (Robinson and van Buijtenen 1979), white spruce (Khalil 1981), and eastern white pine (Kriebel et al. 1972).

This study employed seeds from 64 open-pollinated families of slash pine from parents which have been field tested for 15 years and the goals were 1) to examine relationships among seed weight components and seed size classes, 2) to estimate the magnitude of seed size effects and germination vigor on a variety of seedling growth traits during the first two growing seasons, and 3) to evaluate seed weight components as potential genetic selection criteria for predicting 5- and 15-year breeding values for volume growth.

Materials and Methods

Genetic Material

Open-pollinated seeds were collected from 64 slash pine parents which have been field tested for 15 years by the Cooperative Forest Genetics Research Program (CFGRP). The 64 parents were chosen randomly except that the mean and variance of their breeding values for 15-year volume were constrained to be similar to that of the entire population of approximately 2,500 first-generation selections. Breeding values for these 64 families were predicted using best linear prediction (White and Hodge 1988) from open-pollinated progeny test data with each family being represented in at least 4 test sites (mostly 6-8). Seeds were harvested in 1987 and 1989 from seed orchards owned by ITT Rayonier and Container Corporation of America, located in northeast Florida.

Seed Measurements

Dry weights of the seed coat, gametophyte, and embryo were measured for 60 seeds in each family. In order to obtain a representative sample of the seed size variation inherent to each family, the proportion of large, medium, and small seeds was first determined using sizing screens. Approximately 1,000 to 1,500 seeds were sifted on seed-sizing screens and the percentages of large, medium, and small seeds were recorded. Then, stratified random sampling was used to select a total of 60 seeds per family. For example, if a family had 50% large, 25% medium, and 25% small seeds, then the number of large, medium and small seeds sampled would be 30, 15, and 15, respectively. To determine dry weights of the seed components, seeds were first soaked for 12 h to soften the seed coat. Seed coats were then removed and the embryo and megagametophyte tissue were separated. The inner papery membranes were considered as part of the seed coat (Barnett 1976). Separated seed components were dried at 72° C for 24 h and weighed by size, class, and family, but not by individual seed.

Germination of stratified, sound seed was tested using two replications of 25 seeds per family incubated at 22° C with a 16 h photoperiod. The criterion for germination was a radicle extending at least 5 mm beyond the seed coat. Germinants were counted every day for 14 days at which time germination was considered complete (not necessarily 100%) for all 64 families. Germination speed was assessed using two different criteria: peak value (Czabator 1962) and days to 50% germination (Campbell and Sorensen 1979). Peak value, the mean daily germination rate at the most vigorous time of germination, was calculated according to Czabator (1962). Days to 50% germination was estimated as the number of days (using linear interpolation when necessary) required for a family to reach 50% of its total germination (not necessarily 100%).

Seedling Growth Experiments

Seedlings were grown in two nitrogen (N) regimes (5 ppm and 50 ppm) for two growing seasons in outdoor wooden boxes containing washed sand. The experimental design was a randomized complete block, split-plot design with N regimes as the whole-plot factor and families as the sub-plot factor. Eight boxes were used (2 N regimes x 4 blocks) with 6 seedlings from each of the 64 families randomly assigned to single-tree plots within each box. The total number of planted seedlings per harvest was 3072 (2 N regimes x 4 replications x 6 seedlings per plot x 64 families).

After stratification, seeds were sown in the boxes in April of 1990. Fertilization was delayed for 3 weeks to avoid damping-off fungi (Tinus and McDonald 1979). Nitrogen treatments (ammonium nitrate as the N source) were then imposed using biweekly irrigation with a dilute nutrient solution (DeWald et al. 1992) delivered through a laser-line drip irrigation system. Nutrients other than nitrogen were supplied in proportions similar to those recommended for pine species by Ingestad (1979). The pH of the nutrient solution was adjusted to about 5.5 using concentrated sulfuric acid. Enough nutrient solution was added during each irrigation event to ensure complete replacement of the nutrient supply and seedling boxes were flushed with nutrient-free water every four weeks to prevent buildup of salts. The nutrient solution was sampled periodically and subjected to a complete nutrient analysis. Beginning in October, seedling dormancy was encouraged by gradually increasing the intervals between irrigation events to once per 10 days.

After sowing in April, destructive seedling harvests were conducted at 1) the middle of the first growing season (3 months after sowing), 2) the end of the first growing season (6 months), 3) the beginning of the second growing season (10 months), and 4) the end of the second growing season (18 months). At each harvest, seedlings were excavated by removing one end of each box and gently washing the sand away from the roots. Immediately following harvest, seedlings were cut at the epicotyl scar and taken to a drying oven. Later, dry weights of needle, stem, lateral, and taproot were obtained on a family plot basis over the 6 seedlings within a N-treatment x block x family cell. Three representative shoot traits were chosen to be reported here: stem dry weight, shoot dry weight (stem plus needle), and total height.

Statistical Analyses

An analysis of variance was used to assess family variation in seed weight components, germination peak values, and days to 50% germination. Pearson correlation coefficients were used to determine the phenotypic relationships between family means of seed weight components, and seedling growth traits and field breeding values. To determine the amount of variation in seedling growth traits explained by each seed component and germination vigor indices, separate polynomial regression models were fitted for each seedling growth trait (dependent variable) using each seed weight component and germination peak value and their squares as independent variables. All statistical tests were conducted at the 5% level.

Results and Discussion

Relationships among Seed Weight Components and Seed Size Classes

Analysis of variance indicated significant family differences for all three seed weight components and the two germination vigor indices. All three seed weight components (i.e. embryo, gametophyte, and seed coat) for the large size class were significantly greater than the same components for the medium and small classes, but component weights for the medium and small classes were not significantly different from each other (Table 1-1). The embryo weight/gametophyte weight ratio was 0.13, 0.13, and 0.15 for the small, medium, and large size classes. Thus, it appears that one of the putative advantages of large seed, a higher amount of storage tissue relative to embryo size, is not present in slash pine. Seed coat, gametophyte, and embryo weight expressed as a percentage of total seed weight were approximately 44%, 50% and 6%, respectively and did not vary across size classes. These results are in direct agreement with Barnett (1976), who estimated the same percentages in slash pine and found no variation in the percentages across seed size classes. Data for seed weight components are available for only a few other coniferous tree species. In other southern pine species, proportions of seed coat, gametophyte, and embryo were 56.4%, 37.4%, and 6.2% for loblolly pine, 29.2%, 60.2%, and 10.6% for longleaf pine, and 35.0%, 55.8%, and 9.2% for shortleaf pine (Barnett 1976). In

Table 1-1. Mean weight (mg) and percentage of seed components for each seed size class.

Dry Weight	Mean Weight (mg)[a] Small	Medium	Large	Percent of Total Seed Weight[b] Small	Medium	Large
Seed Coat	16.5	17.1	21.1	43.5	43.3	43.9
Gametophyte	19.0	20.0	24.7	50.0	50.2	49.5
Embryo	2.5	2.6	3.3	6.5	6.5	6.6
Total Seed	38.0	39.8	49.0	100.0	100.0	100.0

[a] All three seed weight components (i.e. embryo, gametophyte, and seed coat) and total seed weight for the large size class were significantly greater than the same components for the medium and small classes, but all components for the medium and small classes were not significantly different from each other ($\alpha = 0.05$).

[b] Seed weight components expressed as a percentage of total seed weight did not vary significantly across the size classes.

Scots pine, seed coat and gametophyte weights were 22 to 27 and 65 to 70% of total seed weight and these percentages were also consistent across different seed sizes (Wrzesniewski 1982).

All family mean correlations among seed weight components were significantly greater than zero. There was a strong relationship between gametophyte weight and embryo weight (r = 0.80), a moderate relationship between seed coat weight and embryo weight (r = 0.68) and a weaker relationship between seed coat weight and gametophyte weight (r = 0.50). A similar correlation (r = 0.51) between seed coat weight and gametophyte/embryo weight has been reported in loblolly pine (Shear and Perry 1985).

Finally, the percentage of large seeds within a family explained only 9% of the variation among families in total seed weight. This result was unexpected, but may be due to the low percentage of large-sized seeds in most families (the percentage of large seed within a family averaged only 28%). Also, because the screen-sizing procedure separated seeds based on diameter only, variation in seed density and architecture may account for the weak relationship between the percentage of large seeds and total seed weight.

Seed Component Relationships with Seedling Growth

Using family means for the 64 families, correlations between seed weight components and seedling growth traits were generally high at 3 months, ranging from 0.06 to 0.80 (Table 1-2). Slight to moderate decreases in correlations were found at 6 and 10 months, depending on the trait; however, most correlations remained statistically significant through the 18-month measurement. In some cases, correlations between seed weight components and shoot weight actually increased from 10 to 18 months in the low N regime. In the high N regime, embryo weight-total height correlations also increased substantially (0.25 to 0.42) from 10 to 18 months.

Table 1-2. Family mean correlations (n = 64) of seed weight components and total seed weight, and germination vigor indices (peak value and days to 50% germination) with seedling shoot traits measured in low and high nitrogen conditions.

	Seed Coat Weight		Gametophyte Weight		Embryo Weight		Total Seed Weight		Peak Value		Days to 50% Germination	
	Low N	High N	Low N	High N	Low N	High N	Low N	High N	Low N	High N	Low N	High N
Stem Dry Weight												
3 Months	0.25	0.38	0.41	0.61	0.53	0.73	0.40	0.60	0.34	0.25	-0.35	-0.29
6 Months	0.46	0.39	0.39	0.33	0.59	0.56	0.49	0.42	0.18	0.18	-0.21	-0.13
10 Months	0.17	0.32	0.28	0.32	0.37	0.31	0.28	0.37	0.14	0.10	-0.10	-0.16
Shoot Dry Weight												
3 Months	0.39	0.50	0.54	0.67	0.68	0.80	0.56	0.70	0.36	0.29	-0.35	-0.32
6 Months	0.42	0.40	0.48	0.46	0.59	0.62	0.53	0.51	0.20	0.19	-0.24	-0.21
10 Months	0.29	0.32	0.42	0.32	0.48	0.31	0.43	0.37	0.14	0.10	-0.13	-0.16
18 Months[a]	0.38	0.07	0.39	0.37	0.57	0.38	0.46	0.29	0.15	0.24	-0.16	-0.24
Total Height												
3 Months	0.06	0.24	0.16	0.40	0.27	0.52	0.15	0.39	0.26	0.20	-0.35	-0.28
6 Months	0.34	0.25	0.13	0.20	0.41	0.33	0.27	0.26	0.05	0.12	-0.09	-0.28
10 Months	0.30	0.23	0.23	0.28	0.38	0.25	0.30	0.31	0.05	0.16	-0.04	-0.28
18 Months	0.26	0.11	0.29	0.28	0.49	0.42	0.34	0.25	0.13	0.19	-0.16	-0.15

[a] Shoot weight at 18 months was measured as fresh weight due to large seedling sizes.

$r \geq |0.21|$ significantly greater than zero at the 10% probability level.

$r \geq |0.26|$ significantly greater than zero at the 5% probability level.

$r \geq |0.31|$ significantly greater than zero at the 1% probability level.

Among the seed weight components, embryo weight consistently had the strongest relationship with seedling growth traits with correlations ranging from 0.27 to 0.80. Seed coat weight showed weaker relationships with growth traits than the gametophyte and embryo components. Correlations between seed weight components and seedling traits were generally higher in the high N regime at 3 months, but by the 10-month or 18-month measurements, correlations were generally higher in the low N regime.

Variation in all seed weight components contributed significantly to variation in all seedling growth traits at 3 months, except for seed coat weight and total height in the low N regime (Table 1-3). The embryo weight component best explained variation in seedling growth traits in both N regimes. Gametophyte weight explained less variation in seedling growth than embryo weight, while seed coat weight explained very little of the variation in seedling growth traits. Total seed weight, by virtue of possessing embryo weight, explained a moderate amount of variation in seedling traits. Slightly higher r^2 values between seed weight components and seedling traits were observed in the high N regime compared to the low N regime. This may be a result of high N conditions enhancing initial differences in seedling size.

Our estimations of seed size effects on seedling growth are generally stronger and longer-lasting than those reported for other coniferous tree species (in comparing results, only those studies employing 10 or more families were used). For example, St. Clair and Adams (1991), employing 39 open-pollinated families of Douglas-fir, found significant correlations between total seed weight and 1- and 2-year height (0.52 and 0.35, respectively) and 2-year dry weight (0.48). Mikola (1984) analyzed 40 full-sib families of Scots pine and found that the correlation between total seed weight and height decreased from 0.60 (significant) in the first year to 0.31 (non-significant) after the second year. In another study employing five fast-growing families and five

Table 1-3. r-square values indicating the percent of variation in seedling growth traits (3 months) that could be accounted for by seed weight components and germination vigor indices.

	Total Height		Stem Dry Weight		Shoot Dry Weight	
	Low N	High N	Low N	High N	Low N	High N
Embryo	0.11	0.29	0.32	0.55	0.50	0.67
Gametophyte	0.04	0.18	0.19	0.40	0.34	0.48
Seed Coat	0.01	0.06	0.08	0.16	0.18	0.29
Total Seed Wt.	0.04	0.19	0.22	0.42	0.38	0.56
Peak Value	0.12	0.08	0.12	0.06	0.13	0.08
Days to 50%	0.17	0.10	0.14	0.10	0.14	0.11

Note: For each seedling growth trait (dependent variable), a linear and quadratic regression model was fitted for each seed weight component (e.g., embryo weight and embryo weight squared as the independent variables). In all regressions, the linear term accounted for most of the explained variation and the quadratic term, while significant, accounted for less then 10% of the explained variation. The lack of fit ($1-r^2$), was signficantly different from zero in all cases and was attributable to family differences in the seedling growth traits not explainable by seed weight components.

slow-growing families of loblolly pine, Waxler and van Buijtenen (1981) found highly significant correlations between total seed weight and height at 8 weeks (0.67) and 10 weeks (0.56) of age, but no significant correlations were observed beyond 10 weeks and correlation values decreased continually to 0.28 by 6 months.

Earlier studies concerning seed size effects in slash pine are contradictory. Langdon (1958) reported no significant differences in height after 1 year of field growth for small, medium, and large seeds, while Shoulders (1961) found that 1-year seedlings from medium-sized seeds had a height advantage over those from larger seed. However, Belcher et al. (1984) reported a highly significant correlation between seed weight and first-year height ($r = 0.84$) in the nursery. Bethune and Langdon (1966) found no seed size effects on nursery height or diameter in southern sources, while in northern sources medium-sized seed produced taller seedlings and greater survival through 6 years than small and large seed. Discrepancies regarding seed size effects on seedling growth are not uncommon and have also been found in loblolly pine (Robinson and van Buijtenen 1979, Cannell et al. 1978, Shear and Perry 1985, Waxler and van Buijtenen 1981), Douglas-fir (Lavender 1958, Bell et al. 1979, St. Clair and Adams 1991), ponderosa pine (Fowells 1953), and eastern white pine (Spurr 1944, Kriebel et al. 1972). The most probable reasons for these discrepancies are differences in the number and origin of seedlots and the competitive nature of the seedling test environment (Kaufmann and McFadden 1960, Campbell and Sorensen 1985, Wrzesniewski 1982).

For most conifer tree species, seed weight effects are strong during the first growing season and may require statistical adjustments such as covariance or regression analysis for seed weight in order to enhance juvenile-mature correlations. However, considering the relatively strong and long-lasting seed weight effects found in this study, statistical adjustments for seed weight effects in slash pine could remove useful genetic variation rather than removing confounding variation. These correlations between seed weights and seedling growth traits are consistent with the hypothesis that family differences in seed weights (particularly embryo weight) are one of the causative factors contributing to genetic variation in seedling growth traits.

Germination Speed

There was significant variation among families for the indices of germination vigor. The mean peak value averaged over families was 12.2 (germination percent per day), ranging from 4.7 to 20.7. These values are slightly lower than peak values reported by McLemore and Czabator (1961) for 29 seedlots of loblolly pine (19.89 to 26.86) and higher than those reported for Pinus caribaea (1.9), Pinus oocarpa (4.7), and Pinus roxburghii (3.2) (Ghosh et al. 1976). Mean days to 50% germination averaged over families was 5.17, ranging from 3.18 to 9.94.

Family mean correlations between germination vigor indices and seedling growth traits were significantly greater than zero at 3 months, but most correlations declined to non-significance thereafter (Table 1-2). Correlations between germination vigor indices and seedling growth traits were substantially lower than those between seed weight components and seedling growth traits. Furthermore, only gametophyte weight among the seed components was significantly correlated with peak value ($r = 0.30$) and days to 50% germination ($r = -0.27$). There were no significant correlations between germination vigor indices and predicted breeding values for field volume growth.

Differences in emergence rates are often cited as the primary mechanism by which seed size effects operate (Dunlap and Barnett 1983). For example, Venator (1973) observed that early germinating seed produced seedlings with 60% more height than seedlings germinating 10 days later. Mexal (1980) estimated that each day of delayed germination in loblolly pine resulted in a 1.7 to 3.3% decrease in first-year diameter. In this study, correlations among germination vigor indices and seedling growth traits diminished substantially during the first growing season, accounting for only 4 to 13% of the variation in growth traits at 3 months and only 0.25 to 8% at 10 months. Thus, germination vigor contributes very little to the magnitude of seed size effects observed in this study, and it appears that seed weight effects may operate through mechanisms other than rapid germination rates. Diminishing effects of emergence rate on seedling growth have also been observed in loblolly pine (Dunlap and Barnett 1983), but not to the degree found in this study.

Seed Component Relationships with Predicted Field Breeding Values

All correlations between family means of seed weight components and predicted field breeding values for 5- and 15-year volume growth were significantly greater than zero. Noteworthy are the high correlations between embryo weight and predicted breeding values (Figure 1). The correlations of embryo weight and field breeding values for volume growth at 5 and 15 year were 0.47 and 0.49, respectively. A scatter plot of embryo weight vs. predicted field breeding values revealed that these correlations are not driven by one or a few families with extremely high or low values for embryo weight and breeding values. To my knowledge, there are no other studies reporting relationships between seed components and predicted additive genetic field breeding values for commercially important tree species.

There are, however, a few reports of long-lasting relationships between total seed weight and height or volume in conifer species. For example, using 75 open-pollinated families of loblolly pine, Robinson and van Buijtenen (1979) found a significant family mean correlation

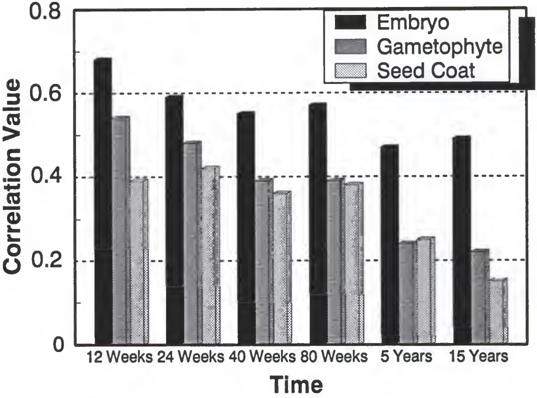

Figure 1-1. Seed weight relationships with seedling shoot weight and predicted field breeding values. Family mean correlations values 3, 6, 10, and 18 months after sowing are between seed weight components and shoot weight (needle plus stem) measured under low N conditions (5 ppm). Correlation values at 5 and 15 years are between family means of seed weight components and predicted field breeding values for volume.

between total seed weight and volume up to age 15 (r = 0.30). Kriebel et al. (1972) observed that seed size effects in eastern white pine accounted for 52% of the height variation in seedling size at age 6. Campbell and Sorensen (1985) hypothesized that seed weight differences of 25% can result in a 12.4% difference in volume at age 8 and 4.1% at age 14.

Our correlations between seed weight components and field breeding values represent genophenotypic correlations if the predicted breeding values are considered as true breeding values (White and Hodge 1991). The genophenotypic correlation (i.e. correlation between the phenotypic value measured and the genetic value being predicted) is the correlation of most interest when evaluating a single trait for indirect selection; the precision of the predicted genetic value from any single indirect observation depends solely on the genophenotypic correlation. Genophenotypic correlations are also the lower limit of the genetic correlation between the indirect selection trait and the target trait.

Seed weight effects are usually manifested through germination vigor and these germination effects often diminish during the first weeks or months of seedling growth. In this study, germination effects did diminish substantially during the first two growing seasons; however, family mean correlations between embryo weight and seedling growth traits remained relatively high throughout the first year, diminished somewhat during the second growing season, but increased again at the end of the second growing season. Embryo weight is apparently related to both seedling size and long-term tree growth. In comparison to seedlings, embryos may lack environmental influences experienced by seedlings and young trees growing in artificial or field environments to predict breeding values.

Genetic correlations of 0.50 or higher, as observed in this study, indicate a moderate degree of genetic pleiotropy or commonness of genes that determine two traits. A genetic relationship between embryo weight and field growth traits may be a causative factor generating relatively high correlations between embryo weight and seedling growth traits, while germination effects on growth were relatively minor. Juvenile-mature correlations are usually assessed between the ages of 1 and 4 which provides the opportunity to reduce the generation interval. When juvenile trait measurements are available at this age, correlations as low as 0.60 may be operationally used in a tree improvement program (Namkoong et al. 1988). Embryo weight has the advantage of being measurable at essentially age zero, providing potentially greater gains per generation than seedling traits. Given that the genetic correlation between embryo weight and breeding values is 0.50 or higher and that the correlation is not driven by one or a few families, embryo weight merits consideration as a potential selection criterion for predicting field breeding values in slash pine. A trait such as embryo weight may also be used in conjunction with other early selection traits in a multiple-trait index, possibly further increasing the juvenile-mature correlation. However, as with any new selection procedure, repeatability of these results must be demonstrated by independent experimentation before operational use in a tree improvement program.

GENETIC PARAMETER ESTIMATES FOR SEEDLING DRY WEIGHT TRAITS AND THEIR RELATIONSHIP WITH PREDICTED BREEDING VALUES IN SLASH PINE

Introduction

In the Cooperative Forest Genetics Research Program (CFGRP), consisting of 9 industry members, 2 state agencies, and the University of Florida, field testing represents a major portion of the budget for the genetic improvement of slash pine. In the first generation of improvement, over 300 field tests were established and measured several times until age 10 at a substantial cost. Currently, the breeding generation interval in the CFGRP is approximately 13-15 years; evaluation for parental worth is at age 8-10 and breeding procedures add another 5 years (White and Hodge 1992). Considering the resources spent in maintaining large numbers of field tests for long periods, research should be aimed at identifying traits early in the tree's life cycle that could facilitate earlier genetic evaluation or reduction of test sizes. In order to be effective, these early selection traits should have high heritabilities (with high precision), high correlations with the target trait, and low phenotypic correlations with each other (White and Hodge 1991).

In both slash and loblolly pines, some studies have found traits which were correlated with mature traits, while other studies have not. These inconsistent results may be due to several reasons. First, in general, a large number of families and individuals are critical for accurate prediction of juvenile-mature correlations (Lambeth 1983). Testing a few families and/or few seedlings per family may yield imprecise estimates of juvenile-mature correlations. Even when the true genetic juvenile-mature correlation is 1.0, sampling errors may cause correlation estimates to be less than 1.0 (Lambeth et al. 1983). For reliable estimates of genetic parameters, many families (at least 50) are required (Huber et al. 1993). Second, when calculating juvenile-mature correlations, many studies have used imprecise estimates of the mature trait rather than precisely estimated additive genetic breeding values from progeny tests on many sites.

Third, seed effects may have a confounding influence on the genetic analysis of early seedling growth by inflating the family variance component leading to biased estimates of heritabilities and genetic correlations (Lambeth 1983, St. Clair and Adams 1991). Fourth, choice of seedling growing environment is critical to maximize the predictive ability and some believe that seedling environments should simulate natural conditions (Waxler and van Buijtenen 1981, Williams 1988). Finally, genophenotypic or family mean correlations with the target traits have been estimated for single juvenile traits at a time. Multiple-trait selection indices combining several juvenile traits will likely provide better predictive ability for the mature trait than single-trait correlations (Foster 1986), particularly if the juvenile traits are correlated with the target, but not phenotypically correlated with each other (White and Hodge 1991).

These factors make it difficult to identify early selection traits that can be used effectively in operational tree improvement programs. Currently, to my knowledge the Western Gulf Forest Tree Improvement Program is the only tree improvement program in the world to employ early selection techniques operationally. This program uses 6-month shoot dry weight to cull the lower 20% of the population of selections, reducing field testing costs by 17% to 40% (Lowe and van Buijtenen 1990).

In this study, I attempt to circumvent some of these problems by a) using a large number of families (64) which have already been extensively field tested for volume growth, b) using best linear prediction to make precise predictions of the parental breeding values for field volume growth (White and Hodge 1988), c) growing the seedlings in two distinct nitrogen (N) environments known to alter seedling trait expression (DeWald et al. 1992), d) analyzing combinations of two- and three-trait selection indices to predict field breeding values, and e) addressing the effects of seed weights on early selection traits and field breeding values. The specific objectives were 1) to estimate family heritability for each trait in limiting (simulating natural conditions) and non-limiting N treatments, 2) to estimate genetic correlations among the traits in the same N treatment, 3) to determine the stability of seedling traits across the two N treatments, i.e. estimate the importance of family x N treatment interaction, and 4) to evaluate all traits singly and in all possible combinations (across three different harvest dates and two N levels) to predict 15-year breeding values for field volume growth.

Materials and Methods

Genetic Material and Seedling Culture

Open-pollinated seeds were collected from 64 slash pine parents which have been field tested for 15 years by the Cooperative Forest Genetics Research Program (CFGRP). The 64 parents were chosen randomly except that the mean and variance of their breeding values for 15-year volume were constrained to be similar to that of the population of the nearly 2500 first-generation selections. Breeding values for these 64 families were predicted using best linear prediction (White and Hodge 1988) from open-pollinated progeny test data; each parent had progeny from at least 4 test locations (mostly 6 to 8 locations). Seeds were harvested in 1987 and 1989 from seed orchards owned by ITT Rayonier and Container Corporation of America, located in northeast Florida.

Seedlings were grown in two nitrogen (N) regimes (5 ppm and 50 ppm) for 10 months in outdoor wooden boxes containing washed sand. The experimental design was a randomized complete block, split-plot design with N regimes as the whole-plot factor and families as the sub-plot factor. Eight boxes were used (2 N regimes x 4 blocks) with 6 seedlings from each of the 64 families assigned to single-tree plots within each box. The total number of planted seedlings per harvest was 3072 (2 N regimes x 4 blocks x 64 families x 6 seedlings). Finally, each box was partitioned into thirds with 3072 planted seedlings in each third to provide material for 3 destructive harvests.

After stratification, seeds were sown in the boxes in April of 1990. Fertilization was delayed for 3 weeks to avoid damping-off fungi (Tinus and McDonald 1979). Nitrogen treatments (ammonium nitrate as the N source) were then imposed using biweekly irrigation with a dilute nutrient solution (DeWald et al. 1992) delivered through a laser-line drip irrigation system. Nutrients other than nitrogen were supplied in proportions similar to those recommended for pine species by Ingestad (1979). The pH of the nutrient solution was adjusted to about 5.5 using concentrated sulfuric acid. Enough nutrient solution was added during each irrigation event to ensure complete replacement of the nutrient supply and seedling boxes were flushed with nutrient-free water every four weeks to prevent buildup of salts. The nutrient solution was sampled periodically and subjected to a complete nutrient analysis. Beginning in October, seedling dormancy was encouraged by gradually increasing the intervals between irrigation events to once per 10 days.

Harvest Dates and Measurements

After planting in April, destructive seedling harvests were conducted in 1) July, the middle of the first growing season (3 months after sowing), 2) October, the end of the first growing season (6 months after sowing), and 3) February, the beginning of the second growing season (10 months after sowing). At each harvest, seedlings were excavated by removing one end of each box and gently washing the sand away from the roots. Immediately following removal from the sand boxes, seedlings were cut at the epicotyl scar and taken to a drying oven. Later, dry weights of needle, stem, lateral roots, and taproot were obtained on a family plot basis pooled over the 6 seedlings within a N-treatment x block x family cell.

Statistical Analyses

To estimate family heritabilities within an N treatment, we used analysis of variance based on plot means (means of the 6 seedlings) within each N treatment. Sequentially adjusted mean squares (SAS Type I) were equated to their expectations to solve for the variance components. Family heritability (h_f^2) was calculated as

$$h_f^2 = \sigma_A^2/\sigma_P^2 = \sigma_f^2/(\sigma_f^2 + \sigma_p^2/4 + \sigma_w^2/4n),$$

where σ_A^2 and σ_P^2 are the additive genetic and phenotypic variances and σ_f^2, σ_p^2, and σ_w^2 are the family, plot, and within-plot variance components all calculated for each trait on a within-N treatment basis. Standard deviations for family heritability estimates were calculated according to Namkoong (1979, pp.232-233). It was not possible to estimate individual-tree heritability because of the pooling of data into family plots, but family heritability is more indicative of potential value in a selection index (White and Hodge 1991).

Type A genetic correlations, measuring the additive genetic correlation between two traits within an N treatment, were estimated from analysis of covariance of plots within an N treatment (Mode and Robinson 1959):

$$r_A = \sigma_{ij}/(\sigma_{fi}^2\ \sigma_{fj}^2)^{0.5},$$

where σ_{ij} is the estimated family covariance between traits i and j from an analysis of covariance, and σ_{fi}^2 and σ_{fj}^2 are the estimated family variances for traits i and j estimated from the previous ANOVA's. Standard errors for Type A genetic correlations were estimated according to Mode and Robinson (1959).

Analyses of variance using data pooled across N treatments were conducted to examine family x N level interactions. Type B genetic correlations, measuring the additive genetic correlation of the same trait measured in two different N treatments, were estimated as

$$r_B = \sigma_f^2/(\sigma_f^2 + \sigma_{ft}^2),$$

where σ_f^2 and σ_{ft}^2 are the family and family x treatment components of variance estimated from the combined analysis of variance across N treatments. Due to the heterogeneity of variances between N treatments, a correction term, K, was used to adjust type B genetic correlations (Dickerson 1962, Yamada 1962):

$$K = (\sigma_{f1} - \sigma_{f2})^2/2,$$

where σ_{f1} and σ_{f2} are the square root of family variance components from the separate analyses of variance for each N treatment. The correction term K was subtracted from σ_{ft}^2 and resulted in σ_{ft*}^2. The adjusted type B genetic correlation, r_B^*, is

$$r_B^* = \sigma_f^2/(\sigma_f^2 + \sigma_{ft*}^2).$$

Standard deviations for the unadjusted type B genetic correlations were estimated according to Mode and Robinson (1959) and used as standard deviation for the adjusted type B correlations (r_B^*).

Indirect prediction indices used to combine seedling traits in two- and three-trait combinations for predicting 5- and 15-year parental breeding values of field volume growth were constructed with best linear prediction methods according to White and Hodge (1991). The correlation between predictions from the juvenile trait index and predicted parental breeding values, Corr($g,\hat{g}$), was used to assess the precision and value of an index. All two- and three-trait combinations were analyzed and those with the highest Corr($g,\hat{g}$) values are reported here.

A correlation between family means of a seedling trait and predicted additive genetic breeding values of volume growth represents genophenotypic correlations if the predicted breeding values are considered as true breeding values (White and Hodge 1991). Genophenotypic correlations are the correlation of interest when evaluating a single trait for indirect selection; the precision of the predicted genetic value from any single indirect observation depends solely on the genophenotypic correlation. Genophenotypic correlations are also the lower limit of the genetic correlation between the indirection selection trait and the target trait (in this case, the mature breeding value). Because these correlations are interpreted as the precision of a single-trait index, they are directly comparable to the multiple-trait indices, i.e. the $\mathrm{Corr}(g,\hat{g})$ values discussed above (White and Hodge 1991).

Results and Discussion

Nitrogen Treatment Effects and Dry Weight Partitioning

At the July harvest (3 months after sowing), there were no significant differences in dry weights between the N treatments (Table 2-1). Because these seedlings were small (less than one-half gram), seed nutrient reserves may have precluded any N treatments effects. During the late summer months, from July to October, total seedling weight increased much more rapidly in the high N treatment (22-fold increase in total weight) compared to the low N treatment (7-fold increase in weight) (Table 2-1). Thus, for all traits measured in October, significant differences across N treatments were observed. DeWald et al. (1992) also observed dramatic differences in slash pine seedlings grown for 6 months under low and high N conditions. Considerable growth also accrued during the over-winter period (October to February); total seedling biomass more than doubled in both N treatments (Table 2-1). In fact, in both N treatments, more total seedling biomass accrued during the winter months (17 weeks) than during the late summer months (13 weeks).

Table 2-1. Overall treatment means, family heritability estimates (h_f^2), and type B genetic correlations (r_B^*) of dry weights measured at 3 harvest dates and 2 growth increments on seedlings of 64 slash pine families grown in low N (5 ppm) and high N (50 ppm) treatments. Standard deviations in parentheses.

	Overall Means		h_f^2		r_B^*
	Low N	High N	Low N	High N	
3-Month Harvest (July)					
Needle	0.18	0.19	0.82 (0.04)	0.84 (0.03)	1.04 (0.11)
Stem	0.04	0.04	0.82 (0.04)	0.84 (0.03)	0.96 (0.14)
Taproot	0.09	0.09	0.88 (0.02)	0.81 (0.04)	1.01 (0.11)
Lateral Root	0.10	0.09	0.80 (0.04)	0.66 (0.07)	0.97 (0.24)
Total Root	0.19	0.18	0.87 (0.03)	0.77 (0.05)	0.98 (0.14)
Total Shoot	0.22	0.23	0.84 (0.03)	0.86 (0.03)	1.02 (0.11)
Total Seedling	0.41	0.41	0.88 (0.02)	0.86 (0.03)	1.00 (0.09)
6-Month Harvest (October)					
Needle	1.71	5.35	0.65 (0.07)	0.77 (0.05)	0.96 (0.23)
Stem	0.42	1.98	0.69 (0.06)	0.74 (0.05)	1.00 (0.43)
Taproot	0.53	1.17	0.75 (0.05)	0.83 (0.03)	1.03 (0.59)
Lateral Root	0.48	0.54	0.72 (0.06)	0.76 (0.05)	0.94 (0.31)
Total Root	1.01	1.71	0.76 (0.05)	0.84 (0.03)	0.86 (0.26)
Total Shoot	2.13	7.33	0.65 (0.07)	0.77 (0.05)	0.92 (0.25)
Total Seedling	3.14	9.04	0.69 (0.06)	0.80 (0.04)	1.01 (0.48)
10-Month Harvest (February)					
Needle	2.41	9.25	0.74 (0.05)	0.75 (0.05)	0.95 (0.47)
Stem	0.91	5.18	0.59 (0.08)	0.71 (0.06)	0.98 (0.72)
Taproot	2.25	4.84	0.58 (0.08)	0.66 (0.07)	0.80 (0.49)
Lateral Root	1.28	2.32	0.50 (0.10)	0.52 (0.10)	1.12 (0.90)
Total Root	3.53	7.16	0.56 (0.09)	0.65 (0.07)	0.90 (0.56)
Total Shoot	3.32	14.43	0.73 (0.05)	0.74 (0.05)	0.96 (0.54)
Total Seedling	6.85	21.59	0.71 (0.06)	0.77 (0.04)	0.93 (0.44)
Late Summer/Fall Growth Increment (July to October)					
Needle	1.53	5.17	0.61 (0.08)	0.76 (0.05)	1.00 (0.46)
Stem	0.38	1.94	0.65 (0.07)	0.73 (0.05)	1.03 (0.62)
Taproot	0.44	1.08	0.69 (0.06)	0.81 (0.04)	0.94 (0.36)
Lateral Root	0.38	0.45	0.63 (0.07)	0.71 (0.06)	0.80 (0.34)
Total Root	0.82	1.53	0.69 (0.06)	0.81 (0.04)	0.89 (0.30)
Total Shoot	1.91	7.11	0.61 (0.08)	0.75 (0.05)	1.01 (0.51)
Total Seedling	2.73	8.64	0.64 (0.07)	0.78 (0.04)	1.00 (0.44)

Table 2-1--continued.

	Overall Means		h_f^2		r_B^*
	Low N	High N	Low N	High N	
Winter Growth Increment (October to February)					
Needle	0.70	3.89	0.43 (0.11)	0.55 (0.09)	0.96 (0.82)
Stem	0.49	3.20	0.35 (0.13)	0.62 (0.08)	1.01 (0.21)
Taproot	1.72	3.67	0.45 (0.11)	0.52 (0.10)	0.81 (0.69)
Lateral Root	0.80	1.79	0.23 (0.15)	0.42 (0.11)	1.31 (1.44)
Total Root	2.52	5.45	0.38 (0.12)	0.55 (0.09)	0.90 (0.78)
Total Shoot	1.19	7.09	0.45 (0.11)	0.59 (0.08)	1.00 (0.85)
Total Seedling	3.71	12.54	0.52 (0.10)	0.61 (0.08)	0.95 (0.66)

Nitrogen treatments also affected dry weight partitioning among the shoot and root components of growth. At the three-month harvest (July), the needle, stem, taproot, and lateral root components composed about 45, 10, 23, and 22 percent, respectively, of the total seedling biomass in both N treatments (Figure 2-1). Three-month shoot/root ratios were approximately 1.2 in both N treatments (Table 2-1). However, during late summer growth increment (July to October), the high N treatment resulted in relatively more needle and stem biomass and less root biomass (particularly lateral root) compared to low N. Percentages of total October biomass for needle, stem, taproot, and lateral root components were 54, 13, 17, and 16% in the low N treatment and 57, 24, 13, and 6% in the high N treatment (Figure 2-1). The October shoot/root ratio was over twice as high in the high N treatment than in the low N treatment (Table 2-1). In comparison to loblolly pine grown for 6 months under low N conditions (Li et al. 1991), slash pine seedlings have relatively more needle biomass and less stem biomass, while root biomass was the same for both species. Biomass distributions were similar for both species in the high N treatment (Li et al. 1991).

Many studies in conifer seedlings have reported increasing shoot/root ratios with increasing availability of N (review by Linder and Rook 1984, Wanyancha and Morgenstern 1987, Li et al. 1991, DeWald et al. 1992). In this study, the increase in shoot/root ratio during the summer months for both N treatments was due to a relatively greater increase in shoot weight (mostly stem) and a lesser increase in root weight (mostly lateral root). Our six-month shoot/root ratios are very similar to those observed in comparable experimental conditions for loblolly pine (Li et al. 1991, Waxler and van Buijtenen 1981) and slash pine (DeWald et al. 1992).

Shifts in dry weight partitioning were also observed during the over-winter months (October through February). The needle weight component decreased to 35% and 43% of total

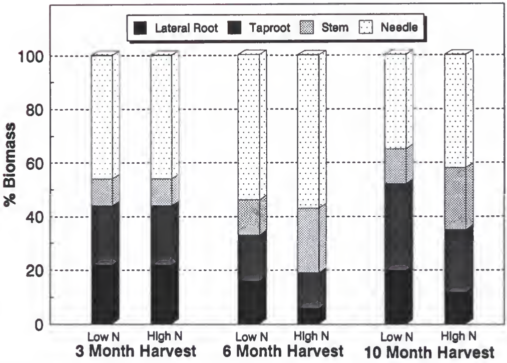

Figure 2-1. Biomass components (needle, stem, taproot, lateral root) as a percentage of total biomass for seedlings of 64 open-pollinated families of slash pine grown in low and high N treatments and harvested at 3, 6, and 10 months after sowing.

biomass in the low and high N treatments, respectively, while the relative stem weight component did not change (Figure 2-1). Root weight components increased substantially during the winter, particularly taproot weight. These shifts in biomass to the root weight components as a fraction of total biomass caused marked decreases in shoot/root ratios to 0.94 in the low N and to 1.93 in the high N. In the low N treatment, 70% of the over-winter biomass increment was attributed to root growth (mostly taproot), while only 30% was due to shoot growth. In the high N treatment, root and shoot growth each contributed about equally to the over-winter biomass increment.

Conifer seedlings and saplings growing in mild climates may often exhibit substantial biomass increments during the winter months. In slash pine, Kaufman (1968) observed near-maximum lateral root growth in slash pine saplings during the winter months of 1964-66. Also in slash pine, Comerford et al. (1987) observed significant increases in needle weight during winter months in 12 stands ranging from 3 to 12 years of age. Significant over-winter growth has also been observed in scots pine saplings (Rutter 1957), and loblolly pine (Smith et al. 1971, Rousseau, unpubl. data). Presumably, overwinter biomass accretion in coniferous trees is due to sustained nutrient uptake (Margolis and Waring 1986, Comerford et al. 1987) and photosynthetic activity (Rook 1985, Teskey et al. 1993) fostered by mild temperatures.

Teskey et al. (1993) have documented relatively high winter rates of net photosynthesis in mature trees of slash pine. Photosynthetic activity in slash pine is primarily driven by photosynthetically active radiation and exhibits low seasonality (Teskey et al. 1993). Respiration rates are approximately 2.4 times lower during the winter months than in the hot summer months. Thus, relatively high photosynthetic rates combined with lower winter respiration rates foster substantial winter carbon gain (Teskey et al. 1993). In a mature slash pine tree, winter-produced carbon reserves are stored in coarse roots (particularly the taproot) which are available for spring growth (Smith et al. 1971, Gholz and Cropper 1991). In support of this hypothesis, marked increases in taproot weight during the winter period were observed in our study.

Family Effects and Family Heritability Estimates

Three months after sowing (July), all seven dry weight traits had significant family differences. Six months after sowing (October), there were significant family differences for needle, tap root, lateral root, and total root dry weights, while dry weights for stem, shoot, and total seedling had non-significant family differences. Family differences were significant for all dry weight traits measured in February.

Family heritability estimates (h_f^2) for seedling dry weight traits at 3 months were high (mostly > 0.8), and in general, declined only slightly thereafter (Table 2-1). At 6 (October) and 10 months (February), family heritability estimates were generally higher than 0.6 in both N treatments. Family heritability estimates for the July to October growth increment were also relatively high, but h_f^2 values for the overwinter growth increment were lower, ranging from 0.23 to 0.62 (Table 2-1).

Standard deviations of the h_f^2 estimates (Table 2-1), measuring their precision of estimation, were relatively low (mostly below 0.10). The standard deviations increased slightly in the later two harvests, but still remained relatively low. High heritabilities and low standard deviations may be due to uniform environmental conditions in the seedling boxes.

Family heritability estimates for our dry weight traits were generally higher in both N treatments than those estimated for 12 shoot traits (such as diameter, number of flushes, cyclic growth, stem units, etc.) on the same seedlings at 6 months (Smith et al. 1993b). A comparison with loblolly pine results can be made with Li (1989) who estimated genetic parameters from seedlings of 23 open-pollinated families grown for approximately 6 months using the same two N treatments as our study (5 and 50 ppm). Overall, Li (1989) observed much higher h_f^2 estimates in the low N treatment compared to high N, while h_f^2 estimates in our study were not different between N treatments.

Declining family heritability estimates observed throughout the measurement period were due to phenotypic variances increasing more rapidly than additive variances. For example, in low N treatment, average additive variance for the seven dry weight traits increased by approximately 100-fold between the first and second harvest, while average phenotypic variance increased by 200-fold. Furthermore, between the 6- and 10-month measurements, average additive variance increased only by 10-fold, while average phenotypic variance increased by over 100-fold. Similar patterns were observed in the high N treatment. Our results agree with those of Franklin (1979) who observed high heritability estimates for slash pine during the first growing season, but declining h^2 estimates thereafter. In that study (Franklin 1979), heritability estimates were high during the first growing season, followed by a lag period during the second and third growing seasons and then an increase in heritability from age 3 until maturity.

Genetic Correlations among Seedling Traits and Family x N Treatment Interaction

Type A genetic correlations (r_A) measure the degree of genetic similarity (commonness of genes) between two different traits measured on the same seedlings. Type A correlations for pairs of traits in both N treatments for the 3- and 6-month harvests were very high, mostly near 1.0 (Table 2-2). For traits measured at 10 months (February), r_A values were again high in the low N treatment, but were generally lower in the high N treatment than for the previous two harvests. Overall, none of the type A correlations among dry weights in any of the harvests were statistically different from 1.0.

Our r_A estimates for dry weight traits measured at six months were generally higher than those estimated among 12 shoot/phenology traits measured on the same seedlings (Smith et al. 1993b). Lower genetic correlations may be expected among the shoot/phenological traits because these traits are morphologically more diverse than dry weight traits. Our estimates of r_A values are similar to those estimated by Li (1989) for dry weight traits in loblolly pine seedlings (none were significantly lower than 1.0).

Type B genetic correlations measure family x N treatment interaction effects caused by changes in family rankings. Type B genetic correlations for all traits in all 3 harvests were either close to 1.0 or not significantly different from 1.0 (Table 2-1); thus, there were no statistically significant changes in family rankings across the N treatments. However, there were significant family x N treatment interaction effects (as measured by a pooled ANOVA across N treatments) for stem, shoot, and total seedling weight in the July harvest and all for traits in the October harvest, indicating interaction due to scale effects (i.e., changes in phenotypic variances across N treatments). Significant family x treatment effects are common in conifer seedling studies and have been reported in loblolly pine (Roberds et al. 1976, Li 1989), Douglas-fir (Bell et al. 1979), black spruce (Maliondo and Krause 1985), tamarack (Wanyancha and Morgenstern 1987) and in slash pine (Pritchett and Goddard 1967, Jahromi et al. 1976, and DeWald et al. 1992).

The type B genetic correlations for 6-month dry weight traits were similar to those of shoot/phenology traits measured by Smith et al. (1993). Hodge and White (1992) have observed moderate amounts of family x site interaction for 5 through 15-year height and volume (average r_B between two sites = 0.65). Our results indicate that there is little family x N treatment

Table 2-2. Type A genetic correlations (with standard deviations) of dry weights measured at 3 harvest dates on seedlings of 64 slash pine families grown in low N (above diagonal) and high N (below diagonal) treatments.

	Needle	Stem	Taproot	Lateral Root	Total Root	Total Shoot	Total Seedling
3-Month Harvest (July)							
Needle	1	0.88±0.23	0.96±0.25	0.91±0.28	0.96±0.26	0.99±0.25	0.99±0.25
Stem	0.89±0.24	1	0.81±0.22	0.74±0.24	0.79±0.23	0.93±0.24	0.88±0.23
Tap Root	0.99±0.25	0.91±0.23	1	0.89±0.27	0.96±0.26	0.95±0.25	0.97±0.25
Lateral Root	0.89±0.24	0.80±0.22	0.89±0.23	1	0.98±0.30	0.89±0.27	0.95±0.28
Total Root	0.96±0.24	0.88±0.23	0.97±0.24	0.97±0.25	1	0.94±0.25	0.98±0.26
Total Shoot	0.99±0.26	0.93±0.24	0.99±0.25	0.88±0.24	0.96±0.24	1	0.99±0.25
Total	0.99±0.25	0.91±0.23	0.99±0.24	0.94±0.24	0.99±0.24	0.99±0.24	1
6-Month Harvest (October)							
Needle	1	0.77±0.26	0.82±0.26	0.75±0.26	0.83±0.27	0.98±0.33	0.95±0.31
Stem	0.89±0.26	1	0.89±0.27	0.79±0.27	0.89±0.27	0.86±0.28	0.89±0.28
Tap Root	0.91±0.25	0.95±0.26	1	0.78±0.24	0.95±0.27	0.87±0.27	0.92±0.22
Lateral Root	0.90±0.26	0.90±0.26	0.87±0.25	1	0.93±0.28	0.79±0.27	0.86±0.27
Total Root	0.93±0.25	0.96±0.27	0.99±0.26	0.94±0.26	1	0.88±0.28	0.95±0.29
Total Shoot	0.99±0.27	0.95±0.27	0.95±0.26	0.92±0.26	0.97±0.26	1	0.98±0.32
Total	0.98±0.27	0.96±0.27	0.96±0.25	0.93±0.26	0.98±0.26	1.00±0.27	1
10-Month Harvest (Februrary)							
Needle	1	0.99±0.33	1.02±0.34	0.89±0.33	1.03±0.34	1.00±0.30	1.00±0.30
Stem	0.96±0.28	1	1.10±0.39	0.99±0.39	1.11±0.39	0.99±0.34	1.03±0.35
Tap Root	0.66±0.23	0.72±0.25	1	0.80±0.32	0.98±0.35	1.05±0.34	0.99±0.33
Lateral Root	0.55±0.26	0.71±0.31	0.97±0.38	1	0.90±0.35	0.92±0.33	0.89±0.33
Total Root	0.62±0.23	0.72±0.26	1.00±0.33	0.96±0.38	1	1.06±0.34	1.02±0.34
Total Shoot	0.99±0.28	0.98±0.29	0.69±0.25	0.62±0.28	0.67±0.27	1	1.01±0.30
Total	0.93±0.26	0.96±0.28	0.88±0.27	0.83±0.32	0.86±0.33	0.95±0.39	1

interaction in dry weight traits caused by changes in family rankings, i.e. the traits are genetically stable across treatments.

The disadvantage of a high type B correlation is a reduction in the number of potential early selection traits. For example, 3-month needle dry weight has a type B genetic correlation of approximately 1.0. Thus, needle dry weight in the low and high N treatments are genetically the same and therefore, in an early selection index, needle weight can be considered only one trait instead of two.

Single-Trait Correlations with Breeding Values

Genophenotypic correlations ($\mathrm{Corr}(g,\hat{g})$) between single dry weight traits and predicted field breeding values at 5 years were similar to those at 15 years (Table 2-3). Also, most genophenotypic correlations were slightly higher in the high N treatment than in the low N treatment for both 5- and 15-year breeding values, although these differences were not statistically significant. For evaluating which traits could be most useful for early selection, we have referred exclusively to correlations of seedling traits with 15-year breeding values.

Genophenotypic correlations were highest at 3 months with most values greater than 0.40. Dry weight traits from the October harvest and from the July to October growth increment had lower genophenotypic correlations than for the July harvest. Genophenotypic correlations using the overwinter growth increment to predict 15-year volume were relatively low; only about one-half of these genophenotypic correlations were statistically greater than zero.

Several genophenotypic correlations from the 3-month harvest (July) are near 0.50 and may be useful in a genetic improvement program for slash pine. These correlations between family means of seedling traits and additive genetic breeding values represent genophenotypic

Table 2-3. Genophenotypic correlations (n = 64) of dry weights measured at 3 harvest dates and 2 growth increments with 5- and 15-year predicted field breeding values for slash pine 64 families grown in low and high N treatments.

	Correlation with 5-Year Breeding Value[a]		Correlation with 15-Year Breeding Value	
Dry Weight Trait	Low N	High N	Low N	High N
3-Month Harvest (July)				
Needle	0.36	0.37	0.39	0.42
Stem	0.33	0.39	0.32	0.42
Taproot	0.42	0.44	0.45	0.47
Lateral Root	0.35	0.30	0.42	0.40
Total Root	0.40	0.38	0.46	0.45
Total Shoot	0.37	0.39	0.39	0.43
Total Seedling	0.40	0.39	0.45	0.45
6-Month Harvest (October)				
Needle	0.15	0.31	0.18	0.34
Stem	0.22	0.22	0.24	0.24
Taproot	0.20	0.31	0.23	0.33
Lateral Root	0.23	0.38	0.34	0.41
Total Root	0.23	0.35	0.30	0.38
Total Shoot	0.17	0.32	0.20	0.35
Total Seedling	0.20	0.33	0.24	0.36
10-Month Harvest (February)				
Needle	0.21	0.05	0.17	0.03
Stem	0.14	0.14	0.11	0.13
Taproot	0.16	0.24	0.21	0.31
Lateral Root	0.26	0.25	0.36	0.32
Total Root	0.19	0.09	0.15	0.07
Total Shoot	0.20	0.25	0.28	0.33
Total Seedling	0.20	0.17	0.22	0.20
Late Summer/Fall Growth Increment (July to October)				
Needle	0.13	0.30	0.15	0.33
Stem	0.20	0.32	0.23	0.34
Taproot	0.16	0.29	0.20	0.31
Lateral Root	0.18	0.37	0.28	0.39
Total Root	0.18	0.33	0.26	0.36
Total Shoot	0.15	0.32	0.18	0.34
Total Seedling	0.17	0.33	0.21	0.35

Table 2-3--continued.

Dry Weight Trait	Correlation with 5-Year Breeding Value Low N	Correlation with 5-Year Breeding Value High N	Correlation with 15-Year Breeding Value[a] Low N	Correlation with 15-Year Breeding Value[a] High N
Winter Growth Increment (October to February)				
Needle	0.17	-0.10	0.09	-0.15
Stem	0.07	0.05	0.03	0.04
Taproot	0.14	0.21	0.19	0.29
Lateral Root	0.21	0.21	0.29	0.28
Total Root	0.14	-0.04	0.08	-0.07
Total Shoot	0.16	0.22	0.23	0.30
Total Seedling	0.16	0.08	0.16	0.10

[a] Genophenotypic correlations are identical to Corr($g,\hat{g}$) of a multiple-trait predictive index (White and Hodge 1991). $r \geq |0.21|$ significantly greater than zero at the 10% probability level.
$r \geq |0.25|$ significantly greater than zero at the 5% probability level.
$r \geq |0.31|$ significantly greater than zero at the 1% probability level.

correlations if the predicted breeding values are considered as true breeding values (White and Hodge 1991). The genophenotypic correlation is the correlation of interest when evaluating a single trait for indirect selection; the precision of the predicted genetic value from any single indirect observation depends solely on the genophenotypic correlation. The genophenotypic correlation is also the (absolute) lower limit of the genetic correlation between the indirect selection trait and the target trait (in this case, the mature breeding value). Because these correlations are interpreted as the precision of a single-trait index, they are directly comparable to the multiple-trait indices, i.e., comparable to the $\mathrm{Corr}(g,\hat{g})$ values discussed below (White and Hodge 1991).

At present, there are very few studies that report genophenotypic correlations between first or second-year traits, and field breeding values for a large number of families. Most early selection studies have reported correlations calculated with phenotypic or family means of parental selections or have used few families when calculating genophenotypic correlations. Our $\mathrm{Corr}(g,\hat{g})$ values are slightly higher than those of phenology traits measured on the same seedlings/families as our study (Smith et al. 1993b). Our results are similar to those estimated by Foster (1986) who found a $\mathrm{Corr}(g,\hat{g})$ value of 0.41 between second-year height and 15-year volume in loblolly pine. Bastein and Roman-Amat (1990) reported a high genophenotypic correlation between 2-year height and additive breeding values for height at age 15 (0.78), but used only 15 families.

The successive declines in genophenotypic correlations at 6 and 10 months may be related to seed effects. For most conifer tree species, seed weight effects are strong during the first few months and may require statistical adjustments such as covariance analysis to enhance juvenile-mature correlations. However, using these same 64 families, Surles et al. (1993) found strong and long-lasting seed effects. Embryo weight, in particular, was highly correlated (on a family mean basis) with seedling biomass and moderately correlated with 15-year breeding values ($r \approx 0.50$). Correlations between seed weights and seedling growth traits are consistent with the hypothesis that family differences in seed weights (particularly embryo weight) are one of the causative factors contributing to genetic variation in seedling growth traits. Thus, statistical adjustments for seed weight effects in slash pine could remove useful genetic variation rather than removing confounding variation (Surles et al. 1993b).

Multiple-Trait Indices

$\mathrm{Corr}(g,\hat{g})$ expresses the correlation between predicted breeding values ($\hat{g}$) from finite, indirect tests having experimental error with true breeding values (g) assumed to have no error because they were predicted from many field tests. Therefore, $\mathrm{Corr}(g,\hat{g})$ expresses the selection efficiency of finite, indirect early testing compared to direct testing in an infinite number of progeny test sites at age 15. Also, for a given selection intensity, $\mathrm{Corr}(g,\hat{g})$ is the genetic gain in 15-year volume achievable from indirect selection at year one relative to the maximum possible gain achievable from direct selection at 15 years (White and Hodge 1991). In our case (Table 2-4) use of the best two-trait juvenile index to select the best families indirectly for volume at age 15 is expected to achieve 52% ($\mathrm{Corr}(g,\hat{g}) = 0.52$) of the genetic gain compared to perfect selection based on true 15-year breeding values that are known without error.

Two-trait indices that combined seedling traits from either the July harvest or from the October harvest had $\mathrm{Corr}(g,\hat{g})$ values only 0.01 or 0.02 higher than the highest single-trait $\mathrm{Corr}(g,\hat{g})$ values (Table 2-4). For example, the highest genophenotypic correlation in the low N treatment of the July harvest was 0.46 (total root weight). Adding lateral root weight to the index increased Corr($\hat{g}$,g) by only 0.01. For the February harvest, adding a second trait increased Corr(g,$\hat{g}$) values by 0.04 in the low N treatment and by 0.05 in the high N treatment. Combining traits across N treatments from any single harvest also increased Corr(g,$\hat{g}$) values by only 0.01 to 0.03. The best correlation with breeding values (0.52) was achieved by combining traits from all three harvests and both N treatments. Three-trait indices (not shown) increase Corr(g,$\hat{g}$) values by only 0.01 (or less) over values for two-trait indices.

Root weight traits tended to dominate the multiple-trait indices. These traits occurred at least once in every index shown in Table 2-4. Root weight traits were also present in most of the top-ranked indices for each harvest-N treatment(s) combination.

Addition of multiple traits to a predictive index will always result in at least a small increase in Corr(g,$\hat{g}$). The increase in Corr(g,$\hat{g}$) will be larger: 1) by adding traits that are weakly correlated with each other and strongly correlated with the genetic value of the target trait, or 2) by adding traits which are strongly correlated with each other, but weakly correlated with the target trait genetic value (White and Hodge 1991). Corr(g,$\hat{g}$) values from the July and October seedling traits were only slightly higher than the best single-trait correlation. This was because traits measured in these harvests were highly genetically correlated with each other (high Type A correlation) and about equally correlated with the breeding values. Combining traits across the different harvests did increase Corr(g,$\hat{g}$) because these traits were less genetically correlated than traits within a harvest.

Our best two-trait Corr($\hat{g}$,g) value (0.52) was slightly higher than the best two-trait value estimated by Smith et al. (1993) using first-year shoot/phenology traits (0.49). Because Type A correlations among our traits were very high, Corr($\hat{g}$,g) values for three-trait indices (0.525) did not increase significantly over values for two-trait indices (0.521). Due to lower Type A

Table 2-4. Correlations (Corr($g,\hat{g}$)) between 'true' breeding values for 15-year volume growth and those predicted using early selection indices composed of combinations of dry weight traits measured at 3 harvest dates in low and high nitrogen (N) treatments.

	Low N Treatment		High N Treatment		Both Treatments	
	Corr($g,\hat{g}$)	Trait(s)	Corr($g,\hat{g}$)	Trait(s)	Corr($g,\hat{g}$)	Trait(s)
3-Month Harvest (July)						
Best One-Trait Correlation[a]	0.46	Total Root	0.47	Taproot	0.47	Taproot-High N
Best Two-Trait Index	0.47	Total Root Lateral Root	0.48	Taproot Needle	0.49	Taproot-High N Root-Low N
6-Month Harvest (October)						
Best One-Trait Correlation	0.34	Lateral Root	0.41	Lateral Root	0.41	Lateral Root-High N
Best Two-Trait Index	0.35	Lateral Root Needle	0.42	Lateral Root Stem	0.43	Lateral Root-Low Lateral Root-High N
10-Month Harvest (February)						
Best One-Trait Correlation	0.36	Lateral Root	0.32	Lateral Root	0.36	Lateral Root-Low N
Best Two-Trait Index	0.40	Lateral Root Stem	0.37	Total Root Needle	0.40	Lateral Root-Low N Stem-Low N
All Harvests (3, 6, 10-Month) and Growth Increments (Late Summer/Fall and Winter)						
Best One-Trait Correlation	0.46	Total Root-1[a]	0.47	Taproot-1	0.47	Taproot-1-High N
Best Two-Trait Index	0.50	Taproot-1 Taproot-2	0.51	Taproot-1 Needle-3	0.52	Taproot-1-High N Needle-2-Low N

[a] Genophenotypic Correlation

Note: The traits most prevalent in the best 25 prediction two-trait indices are list first (on top).

correlations among shoot/phenology traits, $\mathrm{Corr}(\hat{g},g)$ from Smith et al.'s best three-trait index was increased to 0.56, compared to 0.52 from the best two-trait index.

Middle-ranked families may have a tendency to change ranks between juvenile and mature environments. Thus, early selection indices may be more efficient at ranking families in the upper and/or lower ranks (Carter et al. 1990). For operational use, the overall juvenile-mature correlation may be less important than proper ranking of the upper and lower families. Correct classification of upper families may assist assortative mating of the 'elite' parents, while correct classification of lower families is useful for excluding some parents from progeny field tests to decrease testing costs.

To determine if the best early selection index more precisely predicted the 15-year breeding values of the lower- or upper-ranked parents used in this experiment, selection efficiencies were calculated for selecting the top and bottom 10%, 25%, and 50% of the parents. For example, to calculate the selection efficiency of selecting the top 10%, the top 6 parents were selected according to the best early selection index ($\mathrm{Corr}(g,\hat{g}) = 0.52$) and compared to the top 6 families (out of 64) according to the known 'true' breeding values. The true breeding values of the group selected using the early selection index were averaged and divided by the average of the group selected based on true breeding values. Also, if the index is equally effective at identifying family rankings throughout the range of true breeding values, then this selection efficiency should approximate 0.52 ($\mathrm{Corr}(g,\hat{g})$ of the best two-trait index).

For the top 10%, 25%, and 50% of families, the early selection index had efficiencies of 0.12, 0.50, and 0.63, respectively and, for the bottom 10%, 25%, and 50% of families, the early selection index had efficiencies 1.00, 0.49, and 0.63, respectively. While the index was ineffective at identifying the top range of families, it was highly effective for the bottom 10% of parents. It correctly identified all 6 of the poorest families as ranked by the assumed 'true' breeding values. The best early selection index used above was built from a 3-month taproot weight in the high N treatment and a 6-month needle weight in the low N treatment. It requires two different harvests and N treatments as well as a costly root measurement. For this reason, selection efficiency was calculated using different combinations of 3-month traits and N treatment(s). The goal was to find an index combining easily measured (shoot) 3-month traits from a single N treatment. The best index (highest overall $\mathrm{Corr}(\hat{g},g)$ value) using only 3-month shoot traits from a single N treatment had an overall $\mathrm{Corr}(\hat{g},g)$ of 0.435 and a 0.64 selection efficiency for the bottom 10% of families. This index was composed of needle weight and shoot weight, both from the high N treatment. All $\mathrm{Corr}(\hat{g},g)$ values from shoot trait indices are lower than for indices employing shoot and root traits. Thus, when indices are limited to shoot traits, some sacrifices are made in the overall gain expected from selection. A higher selection efficiency for the bottom 10% was attained from the best index using all 3-month traits from both N treatments (low N total root weight and high N taproot weight). However, this index still has the problem of employing two N treatments and root measurements.

In summary, candidate traits for early selection should have high heritabilities with low standard deviations, high correlations with the target trait(s), and low correlations with other early selection traits (i.e. low type A genetic correlations). Most of the traits measured in this study had high and precisely estimated family heritabilities, and some had relatively high correlations with the target trait; however, most traits were also highly genetically correlated with each other, which attenuated increases in early selection efficiency from multiple-trait indices. Also, relatively high type B genetic correlations across N treatments were observed for most traits (low genotype x environment interaction). Thus, adding traits either within or across N treatments did little to improve the predictive ability of the selection indices.

Some improvement in the selection efficiency was achieved by combining traits over the three different harvest dates. Unfortunately, the resulting $\mathrm{Corr}(g,\hat{g})$ value (0.52) was not high enough to supplant current methods for evaluating parental worth through field progeny testing. Furthermore, although this index used data from three harvests and two nitrogen treatments, $\mathrm{Corr}(\hat{g},g)$ from a two-trait index was increased only slightly from the best index using 3-month traits (0.49 to 0.52). However, it did identify the bottom 10% of parents with an accuracy of 100% ($\mathrm{Corr}(\hat{g},g)=1.00$) and may be useful in culling parents prior to field testing. With some sacrifice in accuracy, data from 3-month shoot traits in the high N treatment could be used to cull the bottom 10% of families. Culling even the lower 10% of families may significantly reduce progeny testing costs. This culling procedure may also be effective in the evaluation of candidates for infusion into a breeding program.

RELATIONSHIPS AMONG SEED WEIGHT COMPONENTS, SEEDLING GROWTH TRAITS AND PREDICTED BREEDING VALUES IN SLASH PINE

Introduction

The long life cycle of commercially important pine species has been justification for most tree improvement programs to investigate the feasibility of early genetic evaluation. Many of these studies have not been conclusive or repeatable enough to adopt early selection on a operational basis. To our knowledge, early selection has not been used to supplant field testing in any tree improvement program. The only example of operational implementation of early genetic evaluation is the Western Gulf Forest Tree Improvement Program (WGFTIP) which uses 6-month shoot dry weight to cull the lower 20% of genetic candidates to reduce progeny test costs by 17% to 40% (Lowe and van Buijtenen 1990). Before incorporating early selection into their breeding program, WGFTIP conducted several early selection studies employing numerous environmental treatments, growth chambers, nurseries (see Lambeth 1982). Most of these studies used a large number of families.

In the Cooperative Forest Genetics Research Program (CFGRP), several early selection projects have produced some promising results for slash pine. The most important target traits in the CFGRP are volume growth and fusiform rust resistance (White and Hodge 1993). Juvenile-mature correlations between seedling traits and the target traits have been evaluated with Corr($\hat{g}$,g), which can be interpreted as the genetic gain in target trait achievable from early selection relative to the maximum gain possible from direct selection on the target trait (White and Hodge 1991). de Souza et al. (1991) observed moderate Corr($\hat{g}$,g) values for multiple seedling trait indices used for predicting breeding values for fusiform rust resistance at age 10. Some indices had a high efficiency predicting breeding values for the bottom 25% of families ($\mathrm{Corr}(\hat{g},g) = 0.70$), indicating that early selection may play a role in early culling poor-performing parents for fusiform rust resistance. For volume growth, Smith et al. (1993a) observed moderate $\mathrm{Corr}(\hat{g},g)$ values (up to 0.56, meaning 56% gain from early selection compared to perfect selection at maturity) for 3-trait indices containing first-year stem unit traits used in predicting breeding values for volume growth. For indices containing only second-year shoot traits, maximum $\mathrm{Corr}(\hat{g},g)$ values were approximately 0.50 (Smith et al. 1993a). For 15-year volume growth, Surles et al. (1993a) identified some early selection indices employing first-year dry weight traits that were highly effective at identifying the worse performing parents ($\mathrm{Corr}((\hat{g},g) = 0.70$ to 1.00). These studies used a large number of families (64 to 100) which had been extensively field tested for either fusiform rust resistance or volume growth. Based on the above studies the CFGRP has the opportunity to reduce field test sizes for fusiform rust, and possibly volume growth, based on greenhouse or nursery testing alone.

The overall goal of this study was to predict breeding values for 15-year volume growth in the field using indices from many seedling traits measured under limiting and non-limiting nitrogen conditions during the first two years of growth. The specific goals were: 1) to develop early selection indices for the first- and second-generation populations of slash pine, 2) to determine if different sets of indices are necessary for the first- and second-generation populations, 3) to determine the efficiency of selection for the top and bottom 25% of the first- and second-generation populations, 4) to compare the efficiency of a seedling test to different numbers of field tests for predicting breeding values for 15-year volume growth.

Materials and Methods

Genetic Material and Seedling Culture

Open-pollinated seeds were collected from 64 slash pine parents which have been field tested for 15 years by the Cooperative Forest Genetics Research Program (CFGRP). The 64 parents were chosen randomly except that the mean and variance of their predicted breeding values for 15-year volume (BV15) were constrained to be similar to that of the population of the nearly 2,500 first-generation selections. Breeding values for these 64 families were predicted using best linear prediction (White and Hodge 1988) from open-pollinated progeny test data with each family being represented at least 4 test locations (mostly 6 to 8 locations). Seeds were harvested in 1987 and 1989 from seed orchards owned by ITT Rayonier and Container Corporation of America, located in northeast Florida.

Seedlings were grown in two nitrogen (N) regimes (5 ppm and 50 ppm) for 18 months in outdoor wooden boxes containing washed sand. The experimental design was a randomized complete block, split-plot design with N regimes as the whole-plot factor and families as the sub-plot factor. Eight boxes were used (2 N regimes x 4 blocks) with 6 seedlings from each of the 64 families assigned to single-tree plots within each box. The total number of planted seedlings per harvest was 3072 (2 N regimes x 4 blocks x 64 families x 6 seedlings per plot). Each box was sub-divided into quarters to allow 4 destructive harvests (described later) meaning a total of 4 x 3072 = 12,288 planted seedlings.

After stratification, seeds were sown in the boxes in April of 1990. Fertilization was delayed for 3 weeks to avoid damping-off fungi (Tinus and McDonald 1979). Nitrogen treatments (ammonium nitrate as the N source) were then imposed using biweekly irrigation with a dilute nutrient solution (DeWald et al. 1992) delivered through a laser-line drip irrigation system. Nutrients other than nitrogen were supplied in proportions similar to those recommended for pine species by Ingestad (1979). The pH of the nutrient solution was adjusted to about 5.5 using concentrated sulfuric acid. Enough nutrient solution was added during each irrigation event to ensure complete replacement of the nutrient supply and seedling boxes were flushed with nutrient-free water every four weeks to prevent buildup of salts. The nutrient solution was sampled periodically and subjected to a complete nutrient analysis. Beginning in October of the first growing season, seedling dormancy was encouraged by gradually increasing the intervals between irrigation events to once per 10 days.

Seedling Traits

This study incorporates seedling traits from four other papers (Smith et al. 1993a, Smith et al. 1993b, Surles et al. 1993a, Surles et al. 1993b) and other traits not previously published. While complete details for some traits are included in these papers, measurement methods for all seedling traits are described briefly. Data for all traits were collected from four destructive harvests and several non-destructive measurements during the first two growing seasons. All seedling traits were measured on the trees growing in the seedling boxes previously described. Each trait was measured in both the low and high N treatments and considered as separate traits for the analyses.

First, seed weight components (embryo, gametophyte, and seed coat) were measured for each family using a stratified random sample to select 60 seeds per family (details are in Surles et al. 1993b). Then, destructive seedling harvests were conducted in: 1) July 1990, the middle of the first growing season (3-month harvest), 2) October 1990, the end of the first growing season (6-month harvest), 3) February 1991, the beginning of the second growing season (10-month harvest), and 4) October 1991, the end of the second growing season (18-month harvest). Throughout the paper, these destructive harvests will be referred as the 3-, 6-, 10-, and the 18-

month harvests. At each of the first three destructive harvests, dry weights of needle, stem, taproot, and lateral roots were measured on a family plot basis (the 6 seedlings in each family x block combination in each N treatment). Also calculated at each harvest were allometric coefficients and nitrogen use efficiency traits.

Allometric coefficients were calculated for each family at each harvest from dry weight measurements using the model (Bongarten and Teskey 1987, Li et al. 1991):

$$Y_{ij} = b_0 + b_{0i} + b_1X_{ij} + b_{1i}X_{ij} + R_j + e_{ij},$$

where Y_{ij} is the log transformed organ biomass of the ijth plot mean of family i in block j, b_0 and b_1 are average regression coefficients, b_{0i} and b_{1i} are the coefficients for the ith family, X is log(total biomass), R_j is the replication (or block) effect, and e_{ij} is the error. The b_{1i} family regression coefficient is the trait of interest; it represents the relative allocation of biomass to the organ (i.e., higher b_{1i} values indicate more allocation to the organ). Separate allometric analyses were conducted on family plot mean data in each N treatment for the first three (destructive) harvests. Six different allometric models were conducted (needle weight on total weight, shoot weight on total weight, stem weight on total weight, root weight on total weight, root weight on shoot weight, needle weight on shoot weight, and root weight on shoot weight).

Nitrogen use efficiency (NUE) traits were calculated using ratios of dry weight measurements and tissue N contents at each harvest (N concentrations by the micro-Kjeldahl method). Tissue N content was calculated as product of tissue dry weight and N concentration. At each harvest, these traits included total N utilization efficiency (total seedling weight/total N content), needle N utilization efficiency (total seedling weight/needle N content), leaf N use efficiency (needle weight/needle N content), total uptake efficiency (total seedling N content/total seedling weight), N uptake efficiency (total seedling N content/lateral root weight), and translocation efficiency (needle N content/total seedling N content).

In addition to dry weights, allometric coefficients, and N-use traits, other traits were also measured at each harvest. At the 3-month harvest, total seedling height was measured. At the 6-month harvest, additional measurements included stem unit traits (number of stem units and mean stem unit length for free and cyclic growth), number of flushes, diameter (at the epicotyl scar), number of branches for free and cyclic growth, and heights of free and cyclic growth. At the 10-month harvest, additional measurements were diameter, number of flushes, number of branches on free and cyclic growth, and heights (as defined previously). At the 18-month harvest, 5 traits were measured: diameter, total height, total number of flushes, shoot fresh weight, and the total of branches.

Non-destructive height measurements were conducted 9, 13, and 16 months after sowing. Bud-burst dates (time required for the apical bud to extend 2 cm and 6 cm during spring bud burst) were also measured in the spring of the second growing season. Details of 6-month stem-unit analysis, non-destructive height measurements and bud-burst measurements are described by Smith et al. (1993b).

Finally, relative growth rates (RGR) for both total seedling growth and organ growth (needle, stem, shoots, roots) were derived using methods of Causton and Venus (1981). RGR was calculated for the three different between-harvest growth increments: 1) between the 3- and 6-month harvests, 2) between the 6- and 10-month harvests, and 3) between the 3- and 10-months harvests. RGR for total seedling growth was decomposed into its components, net assimilation rate and leaf weight ratio.

For development of selection indices, the same trait in the low and high N treatment was considered two different traits. Overall, taking into account traits from the four destructive harvests and non-destructive measurements, and the RGR traits, 367 different seedling traits were evaluated in indirect prediction indices.

Selection Indices

The general form of a selection index can be represented as (boldface type indicating vectors and matrices):

$$\hat{g} = \mathbf{b}'\mathbf{z},$$

where $\hat{g}$ (a scalar), is the predicted breeding value for 15-year volume growth (ft^3) under field conditions, $\mathbf{z}$ is an n x 1 vector of family means for n seedling traits expressed as deviations from their respective means, and $\mathbf{b}'$ is an n x 1 vector of index coefficients. The vector of index coefficients can be written $\mathbf{b}' = \mathbf{c}'\mathbf{V}$, where $\mathbf{c}'$ is 1 x n containing covariances between the family means in $\mathbf{z}$ and the breeding values being predicted (i.e., 15-year volume growth), and $\mathbf{V}$ is an n x n vector matrix of variances (diagonals) and covariances (off-diagonals) of family means among the seedling traits (White and Hodge 1991).

The sample of 64 parents was chosen to represent the first-generation population of improved slash pine, but different selection indices may be required to predict second-generation material. Thus, a population was created to represent the second-generation population by taking a subset of the 64 families. Specifically, the 16 families with the lowest breeding value for volume growth were deleted from the 64-family first generation population sample. The mean and variance of breeding values in this 48-family second-generation population are very similar to the operational second-generation population consisting of 933 selections (Hodge et al. 1989). For each population, indices were developed separately for the four destructive harvests, first-year traits, second-year traits, and all traits. Because relationships between two or more traits can be complex, it is difficult to evaluate *a priori* which combination of traits will produce good indices. Therefore, a systematic approach was adopted to examine all possible combinations of two-, three-, and four-trait indices at a given measurement period. This is similar to building a regression equation using all possible combinations of regressors.

Three criteria were used to evaluate the early selection indices. First, we calculated Corr($\hat{g}$,BV15), the correlation between predicted breeding values from finite, early selection tests which have error, and 15-year breeding values (BV15) that were derived from many field tests and therefore, were assumed to have no error. In this study, Corr($\hat{g}$,BV15) also expresses the selection efficiency of finite, early testing compared to direct testing across infinite number of sites at age 15. Thus, for a given selection intensity, Corr($\hat{g}$,BV15) is the genetic gain in 15-year volume achievable from early selection relative to the maximum possible gain achievable from direct selection at 15 years (White and Hodge 1991).

$$\mathrm{Corr}(\hat{g},\mathrm{BV15}) = [\mathbf{c}'\mathbf{V}^{-1}\mathbf{c}/\sigma_A^2]^{0.5},$$

where σ_A^2 is the additive genetic variance of the target trait (15-year volume growth), and **c** and **V** are described above.

Second, any index equation selected in step 1 above with a coefficient on a trait opposite to the sign of the genetic correlation between the seedling trait and 15-year volume was eliminated from further consideration. If covariance matrices are poorly estimated, index values might actually be negatively correlated with breeding values (Hill and Thompson 1978). We thought this possibility would be minimized if the coefficients had the same sign as the genetic correlation.

Third, we examined the efficiency of early selection for the top 25% and bottom 25% of the population for volume growth (i.e., selection of the top and bottom 16 families of the first-generation population and top and bottom 12 families of the second-generation population). Selection efficiency (E) of early selection was estimated by comparing the genetic gain from selection based on early selection indices to the maximum expected genetic gain from selection based on the 'true' breeding values for 15-year volume growth (assumed to be equal to the predicted field breeding values, the BV15's) and was calculated as

$$E = (BV15^{*} - BV15)/(BV15^{**} - BV15),$$

where $BV15^{*}$ is the mean breeding value for the families selected based on the early selection index, $BV15^{**}$ is the mean breeding value for the families selected based on field data, and BV15 is the overall mean breeding value for the given group of families.

Finally, indices were developed on the first-generation population sample for predictive ability on the second-generation sample and vice versa. Although an independent sample of families for validating the indices was not available, this testing was aimed at examining the robustness of a given index to predict breeding values for both population samples.

Results and Discussion

Early Selection Using All Seedling Traits

Based on the criteria discussed above, Corr($\hat{g}$,BV15) values between the assumed 'true' breeding values and those predicted from 2- and 3-trait seedling indices are presented in Tables 1 and 2, respectively for the best indices. For the first-generation population, values ranged from 0.29 to 0.58 for 2-trait indices (Table 3-1) and from 0.33 to 0.65 for 3-trait indices (Table 3-2). For the second-generation population values were lower, ranging from 0.13 to 0.49 for 2-trait indices (Table 3-1) and from 0.27 to 0.56 for 3-trait indices (Table 3-2). Corr($\hat{g}$,BV15) for 4-trait indices were only slightly higher than values for 3-trait indices and are not reported.

Corr($\hat{g}$,BV15) values for 3-trait indices were usually 0.04 to 0.07 higher than Corr($\hat{g}$,BV15) values for 2-trait indices. There was a general pattern of slightly higher Corr($\hat{g}$,BV15) values in the low N, but the pattern was not consistent for all measurement periods. Combining traits across N treatments usually resulted in only slight increases in Corr($\hat{g}$,BV15). This can be attributed to high Type B genetic correlations among the seedling traits measured in the same measurement period, but in different N treatments. When all traits

Table 3-1. Estimated correlations between true and predicted breeding values for 15-year volume growth (Corr[$\hat{g}$,g]), and efficiencies of selection for the top and bottom 25% of the test population for volume growth (Top25 and Bot25, respectively). Selection efficiency is the ratio of gain from selection of the top or bottom 25% of parents using the seedling trait index to gain from selection on the 'true' breeding values (assumed to to equal to BV_{15}) for the test population. Results of the best **two-trait** indices are presented for different harvests and for the first- and second-generation populations.

	Efficiency of Selection								
	Low N Treatment			High N Treatment			Both N Treatments		
First Generation	Corr($\hat{g}$,g)	Top25	Bot25	Corr($\hat{g}$,g)	Top25	Bot25	Corr($\hat{g}$,g)	Top25	Bot25
Seed Traits Only	0.53	0.39	0.80	0.53	0.39	0.80	0.53	0.39	0.80
3-Month Harvest	0.50	0.54	0.57	0.51	0.34	0.60	0.52	0.53	0.49
6-Month Harvest	0.44	0.47	0.42	0.44	0.18	0.48	0.50	0.45	0.49
10-Month Harvest	0.50	0.39	0.55	0.47	0.34	0.51	Same as Low N		
18-Month Harvest	0.29	0.24	0.43	0.39	0.43	0.56	0.39	0.43	0.56
First Year	0.54	0.51	0.60	0.53	0.39	0.63	0.55	0.45	0.72
Second Year	0.48	0.52	0.32	0.50	0.35	0.65	0.50	0.55	0.36
All Traits (with seed)	0.58	0.33	0.68	0.55	0.38	0.58	Same as Low N		
All Traits (without seed)	0.58	0.51	0.55	0.56	0.56	0.72	Same as Low N		
Second Generation									
Seed Traits Only	0.29	0.38	0.46	0.29	0.38	0.46	0.29	0.38	0.46
3-Month Harvest	0.45	0.41	0.70	0.32	0.32	0.49	Same as Low N		
6-Month Harvest	0.34	0.39	0.39	0.46	0.57	0.53	Same as High N		
10-Month Harvest	0.31	0.16	0.70	0.30	0.36	0.32	Same as Low N		
18-Month Harvest	0.33	0.15	0.62	0.13	0.26	-0.08	0.33	0.22	0.53
First Year	0.45	0.32	0.47	0.46	0.57	0.52	Same as High N		
Second Year	0.38	0.34	0.41	0.38	0.16	0.57	0.41	0.44	0.61
All Traits (without seed)	0.49	0.36	0.68	0.46	0.57	0.53	Same as Low N		

Table 3-2. Estimated correlations between true and predicted breeding values for 15-year volume growth (Corr[$\hat{g}$,g]), and efficiencies of selection for the top and bottom 25% of the test population for volume growth (Top25 and Bot25, respectively). Selection efficiency is the ratio of gain from selection of the top or bottom 25% of parents using the seedling trait index to gain from selection on the 'true' breeding values (assumed to to equal to BV_{15}) for the test population. Results of the best three-trait indices are presented for different harvests and for the first- and second-generation populations.

	Efficiency of Selection								
	Low N Treatment			High N Treatment			Both N Treatments		
First Generation	Corr($\hat{g}$,g)	Top25	Bot25	Corr($\hat{g}$,g)	Top25	Bot25	Corr($\hat{g}$,g)	Top25	Bot25
Seed Traits Only	0.55	0.64	0.32	0.55	0.64	0.32	0.55	0.64	0.32
3-Month Harvest	0.57	0.46	0.66	0.56	0.41	0.59	0.57	0.53	0.59
6-Month Harvest	0.48	0.18	0.47	0.47	0.24	0.47	0.57	0.60	0.50
10-Month Harvest	0.57	0.45	0.68	0.55	0.56	0.48	Same as Low N		
18-Month Harvest	0.33	0.31	0.38	0.41	0.48	0.50	0.44	0.37	0.55
First Year	0.58	0.50	0.78	0.57	0.48	0.66	0.61	0.46	0.76
Second Year	0.60	0.62	0.66	0.55	0.53	0.48	0.62	0.56	0.70
All Traits (with seed)	0.64	0.53	0.65	0.61	0.56	0.71	Same as Low N		
All Traits (without seed)	0.61	0.51	0.59	0.59	0.49	0.70	0.65	0.56	0.80
Second Generation									
Seed Traits Only	0.35	0.37	0.50	0.35	0.37	0.50	Same as Low N		
3-Month Harvest	0.50	0.41	0.67	0.49	-0.29	-0.07	0.50	0.41	0.67
6-Month Harvest	0.39	0.27	0.55	0.52	0.62	0.50	0.53	0.59	0.69
10-Month Harvest	0.35	0.14	0.49	0.33	0.31	0.34	0.35	0.27	0.76
18-Month Harvest	0.33	0.18	0.57	0.27	0.24	0.45	0.38	0.16	0.48
First Year	0.53	0.42	0.62	0.53	0.62	0.53	Same as Low N		
Second Year	0.42	0.56	0.43	0.46	0.20	0.80	0.49	0.33	0.73
All Traits (without seed)	0.56	0.46	0.61	0.53	0.62	0.53	Same as Low N		

were considered, Corr($\hat{g}$,BV15) values for 3-trait indices were slightly higher with seed traits included (Table 3-2), but Corr($\hat{g}$,BV15) values for 2-trait indices were the same or lower with seed traits included (Table 3-1).

Corr($\hat{g}$,BV15) values estimated in this study were higher than those previously estimated for volume growth (Smith et al. 1993a, Smith 1993b, Surles et al. 1993a) and those estimated for fusiform rust resistance (DeSouza et al 1991). Higher Corr($\hat{g}$,BV15) values in this study can probably be attributed to many more traits available for inclusion in the indices.

Selection efficiencies (E) for the top and bottom 25% of parents (as ranked by the 'true' BV15's) varied widely with each index (Tables 3-1 and 3-2). E values for the top 25% were usually lower than the Corr($\hat{g}$,BV15) values, while E values for the bottom 25% were usually higher than Corr($\hat{g}$,BV15). For several indices, E values for the bottom 25% of parents was 0.70 or higher. Indices with high Corr($\hat{g}$,BV15) values did not necessarily have high E values. For example, the best second generation two-trait index for the 10-month harvest had a high E value (0.70 for the bottom 25%) while having a relatively low Corr($\hat{g}$,BV15) value (0.31).

Early Selection Using the Most Promising Early Selection Traits

The above Corr($\hat{g}$,BV15) values are from indices using all traits available for a growth period. However, in practice, an operational early selection procedure should use only those traits which are easy and inexpensive to measure. Four criteria that would be characteristic of an ideal index were 1) traits requiring only one destructive harvest, 2) traits from either the low or high N treatment (not both), 3) traits measured during the first growing season, 4) traits requiring no lateral root measurement, 5) traits requiring no measurement of nitrogen content, and 6) traits that could be measured non-destructively. While no single index could satisfy all of these criteria simultaneously, I sought indices with one or two desirable attributes. I also attempted to avoid traits that were difficult to interpret biologically and traits having low heritabilities.

To develop the most promising indices, traits satisfying one or more of the above criteria were chosen from the 367 available traits. Then, an analysis was conducted with these traits to calculate Corr($\hat{g}$,BV15)'s and efficiencies of selection for the top and bottom 25%. Separate analyses were again conducted in the first- and second-generation populations. After careful analyses of resulting indices, four first-generation indices and 3 second-generation indices were chosen for further evaluation and possible operational use.

Descriptions of the 9 most promising traits in these indices are in Table 3-3. Family heritability estimates for TAPL, TAPH, FHTL, and HTIL were high (Table 3-4). Family heritabilities for EMBR and MEGA were not estimated because seed weight components for individual seeds were too small to be estimated without large sampling errors. Similarly, heritability estimates were not available for the allometric traits (STTL, NETL, and SHTH) because they were derived from plot mean data for each family.

If a single seedling trait is used to predict volume growth, this correlation between family means and true breeding values (Corr[z_i,BV15]) is equal to the correlation between the predicted and true breeding value, Corr($\hat{g}$,BV15). Thus, EMBR, TAPL, and TAPH would be the best single traits to predict BV15 in the first-generation population and TAPL, TAPH, and HTIL would be the best single traits to predict BV15 in the second-generation population (Table 3-5).

TAPL, TAPH, EMBR, and MEGA were positively correlated with BV15, indicating that larger taproot sizes and larger seed weight components were associated with families with higher breeding values for volume growth. Among the allometric traits, STTL was negatively correlated with BV15, while NETL and SHTH are positively correlated with BV15. A negative correlation between STTL and BV15 means that families allocating less biomass to the stem have higher

Table 3-3. Abbreviations and definitions for first-year slash pine traits used in selection indices.

Trait ID	Description (units)
EMBR	Embryo weight (mg)
MEGA	Megagametophyte weight (mg)
TAPL	Taproot dry weight at 3 months in low N treatment (g)
TAPH	Taproot dry weight at 3 months in high N treatment (g)
STTL	Allometric coefficient at 3 months (stem weight regressed on total weight in low N treatment) (g/g)
NETL	Allometric coefficient at 3 months (needle weight regressed on total weight in low N treatment) (g/g)
SHTH	Allometric coefficient at 3 months (shoot weight regressed on total weight in high N treatment) (g/g)
FHTL	Ratio of free height to total height in the low N treatment at 6 months (cm/cm)
HTIL	Height increment from January to May in the low N treatment (second growing season) (cm)

Table 3-4. For 9 seedling traits, family heritabilities (h^2_f) and correlation with breeding values (Corr(z_i,BV15)) in the first and second generation populations. Data are presented for the first and second generation populations.

	h_f^2		Corr(z_i,BV15)	
Trait	First Generation	Second Generation	First Generation	Second Generation
EMBR	-	-	0.49	0.19
MEGA	-	-	0.27	0.03
STTL	-	-	-0.13	-0.16
NETL	-	-	0.16	0.28
SHTL	-	-	0.22	-0.02
TAPL	0.88	0.78	0.45	0.29
TAPH	0.81	0.86	0.47	0.28
FHTL	0.60	0.56	0.27	-0.04
HTIL	0.58	0.62	0.37	0.31

BV15s than those families allocating more biomass to the stem. Similarly, positive correlations between NETL and SHTH, and BV15 indicates families with more allocation to needles and shoots (respectively) have higher BV15s.

Using only the most promising (easily measured) traits resulted in lower Corr($\hat{g}$,BV15) values than using all available traits (Table 3-5). However, more important to operational breeding programs may be the efficiency of selection in the top and bottom portions of the population. Efficient selection of the top portions of the population (the elite selections) may facilitate more efficient mating schemes, while efficient selection of the bottom portion facilitates early culling of selections. Selection efficiencies for the bottom 25% using the most promising indices (Table 3-5) were similar to E values obtained from indices using all available traits. Thus, there was little compromise in E values by using easily measured traits. For bottom 25% selection, indices 1-4 were best for the first-generation population and index 7 was best for the second-generation population. For top 25% selection, index 6 is best for both populations. No single index developed in either population was efficient for selecting both the top and bottom 25%.

To determine the degree of robustness, indices developed in the first-generation population were tested in the second-generation population and indices developed in the first-generation population were tested in the second-generation population. Indices 3 and 6 were the only indices that were efficient in both populations simultaneously (Table 3-3). Index 3, developed in the first-generation population, is efficient for selection of the bottom 25% of both populations. Index 6, developed in the second-generation population, is efficient at selecting the top 25% in both populations. In fact, E values were higher when the index is applied to the other population. A versatile index such as this may be promising for future use. Similarly, taproot weights and

Table 3-5. The most promising first and second generation selection indices. All indices are tested for predictive ability in the first and second generation populations. Selection efficiency is the ratio of expected gain based on seedling trait selection indices to gain from selection on the 'true' breeding values (assumed to to equal to BV15). Trait abbreviations are defined in Table 3-3.

	Test Population					
	First Generation			Second Generation		
Most Promising Indices	Corr($\hat{g}$,g)	Top25	Bot25	Corr($\hat{g}$,g)	Top25	Bot25
First Generation Indices						
1) $\hat{g} = 24.26(EMBR) - 1.14(MEGA)$	0.53	0.39	0.80	0.24	0.24	0.47
2) $\hat{g} = 24.14(EMBR) - 1.18(MEGA) - 0.10(STTL)$	0.53	0.42	0.72	0.26	0.20	0.54
3) $\hat{g} = 26.68(TAPH) + 0.30(SHTH)$	0.51	0.34	0.60	0.24	0.07	0.64
4) $\hat{g} = 27.77(TAPH) + 0.03(FHTL)$	0.56	0.56	0.72	0.24	0.24	0.24
Second Generation Indices						
5) $\hat{g} = 0.44 + 14.48(TAPL) + 0.65(NETL) - 0.20(STTL)$	0.50	0.41	0.67	0.44	0.45	0.51
6) $\hat{g} = 0.44 + 0.01(HTIL) + 0.68(NETL) - 0.21(STTL)$	0.53	0.72	0.61	0.42	0.55	0.37
7) $\hat{g} = 0.44 + 17.29(TAPL) + 0.52(NETL)$	0.46	0.46	0.49	0.45	0.41	0.70

allometric coefficients appear to be particular robust traits in that they occur in the best indices of both populations (Table 3-3).

These indices, however, do not satisfy all of the criteria for easily measured traits (refer to Table 3-3). For example, all of the indices (except EMBR and MEGA) require root measurements and destructive harvests. Indices 3 and 7 require separate taproot and lateral root measurements. Indices 4 and 6 require two different sets of seedlings because they require an early destructive sample and a later height measurement. Index 4 has one low N trait and one high N trait. On the other hand, some of the indices have the advantages of requiring only one N treatment (indices 2, 3, 5, 6, and 7), requiring only one destructive harvest (indices 2, 3, 5, and 7). Index 1 (EMBR and MEGA) has the distinct advantage of being measurable without growing seedlings.

Index 1 could be particularly useful in culling poor performing infusions because it identifies the worst performing parents for volume growth 80% as efficiently as direct selection at 15 years. EMBR and MEGA have a distinct advantage over other traits because they are measurable before seedling material is available and require about 1 h per family to measure (assuming 60 seeds per family). X-ray technology is now available that could circumvent the need to physically separate seed tissue to assess embryo size. However, before implementation on an operational scale, the relationship between these two traits and breeding values needs verification with different set of families.

Operational Implementation of Early Selection Indices

The CFGRP has recently developed its advanced-generation breeding strategy (White and Hodge 1993). The most important target traits in the CFGRP have been and will continue to be volume growth and fusiform rust resistance. Selection for the second-generation population (933 selections) was completed in 1988 and this population is comprised of 395 backward (first-generation) selections, 318 forward (new second-generation) selections, and 220 new (putatively rust resistant) infusions (Hodge et al. 1989). The 933 selections are sub-divided horizontally into 24 breeding groups (2 groups per cooperator) of 39 selections each. Each breeding group is stratified vertically into three strata. Stratum I of each breeding group contains the top 13 selections (out of 39), stratum II the middle third, and stratum III the bottom third. The strategy calls for placing increasing emphasis on selection in higher strata (i.e., they are involved in more crosses and will be better tested for general combining ability).

New infusions have been incorporated into stratum III of each breeding group along with other lesser tested material. While the 220 new infusions have been screened for fusiform rust resistance at the U.S. Forest Service Rust Screening Center, they have not been field tested for volume growth; nor are there any plans to include them in future field tests. The primary purpose of stratum III selections is to provide genetic material for infusion into the upper strata and to provide a broad genetic base. The breeding strategy calls for crossing each stratum III clone with one stratum I clone (13 crosses per breeding group or 312 total crosses). The goal of these crosses is to make third generation selections from full-sib progeny which received the best alleles from the stratum III selection, combined with alleles from a selection already in the top third of the breeding population. Full-sib families resulting from these crosses will be planted in unreplicated plots containing 50 to 100 seedlings. Forward selections for the third-generation population will be made from the best family plots based on estimates of general combining ability (GCA).

Crossing among stratum I and III selections is already in progress. Thus, there is no opportunity to evaluate the infusions before crossing. However, early selection tests using the indices here could be used to obtain GCA estimates for stratum III selections already crossed.

Then, stratum I x III full-sib families could be evaluated based on GCA estimates from **both** parents. Because infusions would be considered a first-generation population, any of the indices 1 through 4 could be used for this application. These indices will particularly effective in evaluating the infusion population since it is essentially unimproved and is expected to have large numbers of selections with low breeding values. Any future candidates for infusion into the breeding population could be also be tested with these indices. This would allow broadening of the genetic base while ensuring that infusions meet a minimum requirement for volume growth.

After full-sib families have been selected based on GCA estimates, some form of early selection could be used along with other selection criteria (such as phenotypic appearance and flowering) to make within-family selections. Index 1 (the seed index) may be the most expedient way to evaluate individuals within families, particularly if x-ray technology is used.

Another possible application of indices efficient for selecting the bottom 25% is early evaluation of crosses made between stratum I and II selections as well as crosses among stratum II selections. Crosses that performed poorly in early selection tests would then be eliminated from further testing. In future generations, early selection indices which are efficient for evaluating the top 25% of the populations could be used to direct assortative (i.e., crosses among selections good for volume growth) and complementary crossing (i.e., crosses between selections good for rust resistance and selections good for volume growth). Although ancestral information would be available to direct crossing, information on the actual selections involved in crossing may be available only via early selection data. In this scenario, index 6 would be applied because it is efficient for selecting the upper portion of the populations.

When considering early selection indices for operational use, it is important to compare early testing and field testing for predicting breeding values. The efficiency of predicting breeding values increases with both the age and number of field tests (Figure 3-1). Given the

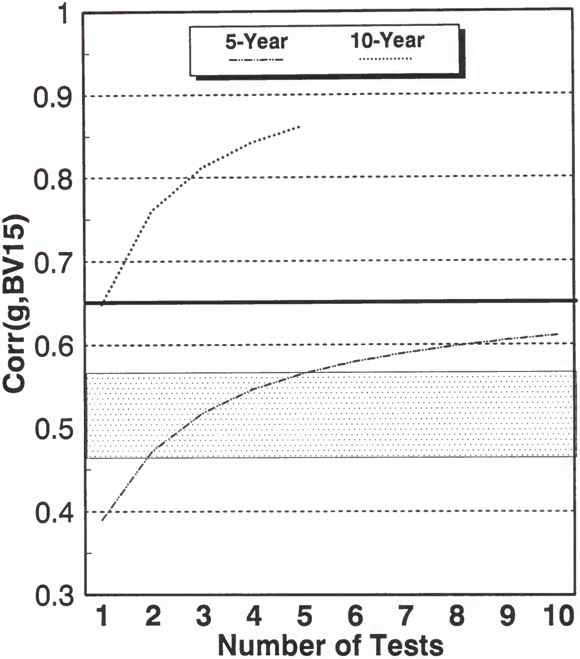

Figure 3-1. Comparison of early testing and different numbers of 5- and 10-year old field tests in predicting breeding values for 15-year volume growth. Shaded area represents Corr($\hat{g}$,BV15) values for the most promising traits. The solid horizontal line at Corr($\hat{g}$,BV15) equal to 0.65 represents the best overall early selection index in the study.

genetic parameters assumed for second-generation field testing (White and Hodge 1993), Corr($\hat{g}$,BV15) values for the most promising indices are equivalent to approximately five or fewer 5-year-old field tests (Figure 1). Maximum Corr($\hat{g}$,BV15) from three-trait indices in this study (0.65) are equivalent to one 10-year field test and better than ten 5-year tests. Thus, another application for early selection indices would be to facilitate seed orchard rouging because early testing could provide estimates of general combining ability before the information could be obtained from field tests. For parents included in only a few field tests (5 or less), early testing may provide better general combining ability estimates than field testing.

In summary, this study has developed several easily-measured early selection indices which can provide alternatives to or augment current testing methods for slash pine in the CFGRP. The indices will probably have more application for culling than for selecting the 'elite'. Before operational use however, the results of this study need to be verified with a different set of families representing the first or second generation population. This verification study would be conducted on a much smaller scale, using some of the 9 most promising traits and only one N treatment. If new early testing data become available, then index coefficients developed in this study can be revised. New predictions of breeding values can be generated by applying the revised coefficients to the old data. Thus, each round of early testing can improve selection efficiency by providing estimates of the $\mathbf{V}$ and $\mathbf{c}$ matrices.

CONCLUSIONS

This study was conducted to investigate early selection for volume growth in slash pine in the Cooperative Forest Genetic Research Program (CFGRP). A total of 367 traits were measured on seedlings from 64 open-pollinated families which had been extensively field tested to predict breeding values for 15-year volume growth. Seedlings were grown in low and high nitrogen (N) treatments (known to alter growth patterns) for two years in outdoor boxes located at the University of Florida's Austin-Cary Forest. Four destructive harvests and several non-destructive measurements conducted throughout the two-year growth period provided data for seedling traits. The study was divided into three stages.

First, seed weight effects on seedling growth and long-term field growth were assessed because these effects can influence early selection efficiency. There were strong relationships between seed weight components (embryo, gametophyte, and seed coat) and seedling growth traits. The strength of the relationship diminished only modestly during the second growing season. Seed weight effects were not exerted through germination vigor as typically observed in conifer seedlings. There was also a moderate relationship between embryo weight and long-term growth. Practical ramifications of this study were that seedling trait data should not be statistically adjusted for seed weight effects because seed weights are related to both seedling size and long-term tree growth. Furthermore, embryo weight should be considered for inclusion in indices for predicting breeding values for volume growth.

In the second stage of the study, genetic parameters were estimated for key dry weight traits measured at the first three destructive harvests. Genetic parameters included family heritability estimates, Type A genetic correlations (different traits measured in the same N treatment), and Type B genetic correlations (same trait measured in the low and high N treatments). The best candidates for early selection have high (and precisely estimated) heritabilities, low correlations with other traits (i.e., low Type A and Type B genetic correlations), and high correlations with volume growth. Most of the dry weight traits had high (precisely estimated) heritabilities and moderate correlations with volume growth. However, most traits also had high Type A and Type B genetic correlations which attenuate increases in early selection efficiency for multiple-trait indices. Dry weight traits from the first harvest were the best candidates for early selection due to relatively high correlations with breeding values.

The third stage of the study, early selection indices built from seed and seedling traits were evaluated with Corr($\hat{g}$,BV15), the genetic gain in target trait achievable from early selection relative to the maximum gain possible from direct selection on the target trait and E, selection efficiency for the bottom and top 25% of the population. Two populations were considered, the 64-families representing the operational first generation population and a 48-family group (subset of 64 first generation families) representing the operational second generation population. Corr($\hat{g}$,BV15) and the two E values were estimated for both populations by harvest, at one year, at two years, and over the entire measurement period. Corr($\hat{g}$,BV15) for indices using traits at a harvest or year were generally 0.50 or higher in the first-generation population and lower in the second generation population. In both populations, E values for the bottom 25% were generally higher than Corr($\hat{g}$,BV15); E values for the top 25% were generally lower than Corr($\hat{g}$,BV15). When indices were limited to easily measured traits (i.e, traits measured at one harvest, in one N treatment, or non-destructive measurements), Corr($\hat{g}$,BV15) values were slightly lower than when all traits were considered. However, E values remained relatively high in both populations. Two of these 'most promising indices' were robust enough to be applied in both the first and second generation populations. One index was efficient at predicting breeding values for the bottom 25% of the populations, while the other was efficient at predicting breeding values for the top 25% of the populations. Practical uses of these indices include: 1) evaluating rust resistant infusions that have been incorporated into the breeding program, but have not yet been tested for volume growth, 2) early evaluation of crosses made to provide material for third generation selection, and 3) providing information for rouging clones already established in seed orchards.

APPENDIX A
VARIANCE OF FAMILY MEANS OF THE 9 MOST PROMISING SLASH PINE TRAITS

	VARIANCE OF FAMILY MEANS	
TRAIT	FIRST GENERATION POPULATION	SECOND GENERATION POPULATION
EMBR	0.00007	0.00058
MEGA	0.06304	0.06387
TAPL	0.00015	0.00014
TAPH	0.00024	0.00020
STTL	0.45238	0.52089
NETL	0.13546	0.14840
SHTH	0.29966	0.32969
FHTL	51.66485	49.23447
HTIL	1017.23713	1070.86785

APPENDIX B
FAMILY MEAN CORRELATIONS AMONG THE 9 MOST PROMISING TRAITS

TRAIT	EMBR	MEGA	TAPL	TAPH	STTL	NETL	SHTH	FHTL	HTIL
EMBR	1.00	0.80	0.72	0.82	-0.15	0.02	0.09	0.11	0.50
MEGA	0.74	1.00	0.56	0.68	-0.16	0.03	0.03	-0.10	0.19
TAPL	0.64	0.47	1.00	0.86	-0.27	-0.09	0.09	-0.01	0.52
TAPH	0.72	0.57	0.84	1.00	-0.18	0.03	0.08	-0.01	0.47
STTL	-0.18	-0.17	-0.29	-0.20	1.00	0.28	0.12	0.05	-0.23
NETL	-0.06	-0.06	-0.17	-0.09	0.39	1.00	-0.02	0.04	-0.20
SHTH	-0.05	-0.07	0.04	-0.02	0.12	-0.02	1.00	0.14	-0.06
FHTL	-0.05	-0.27	-0.16	-0.20	0.08	0.00	0.04	1.00	0.01
HTIL	0.40	0.06	0.44	0.40	-0.26	-0.20	-0.13	-0.01	1.00

NOTE: Family mean correlations above the diagonal are for the first-generation population and those below the diagonal are for the second-generation populations.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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